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A maximalist approach to the systematics of a biological control agent: *Gryon aetherium* Talamas, sp. nov. (Hymenoptera, Scelionidae)

Elijah J. Talamas[1], Jonathan S. Bremer[1], Matthew R. Moore[1], Marie-Claude Bon[2], Zachary Lahey[3], Cheryl G. Roberts[1], Lynn A. Combee[1], Natalie McGathey[1], Simon van Noort[4], Alexander V. Timokhov[5], Evelyne Hougardy[6], Brian Hogg[6]

1 *Florida Department of Agriculture and Consumer Services, Gainesville, FL, USA* **2** *USDA-ARS-EBCL, Montpellier, France* **3** *Department of Evolution, Ecology, and Organismal Biology, The Ohio State University, Columbus, OH, USA* **4** *Iziko South African Museum, Cape Town, South Africa* **5** *Lomonosov Moscow State University, Moscow, Russia* **6** *USDA-ARS-ISPH, Albany, CA, USA*

Corresponding author: Elijah J. Talamas (elijah.talamas@fdacs.gov)

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Abstract

A morphological and molecular analysis of *Gryon* Haliday (Platygastroidea, Scelionidae) was conducted to provide a taxonomic and phylogenetic context for a species under evaluation as a biological control agent of *Bagrada hilaris* (Burmeister) (Hemiptera, Pentatomidae). Our analysis revealed that *Gryon* is polyphyletic and that the biological control agent is not *G. gonikopalense*, a name that was tentatively applied to this species in 2019. We here describe this species as new, *Gryon aetherium* Talamas **sp. nov.**, and resurrect the generic name *Hadronotus* Förster. Morphological characters that delimit our concepts of *Gryon* and *Hadronotus* are presented. Based on morphological characters and multilocus phylogenies, we determined that five presently valid scelionid genera belong within *Gryon*. In total, 15 species are transferred into *Gryon* from these genera, 215 species are transferred from *Gryon* to *Hadronotus*, and 6 species are transferred from *Gryon* to *Dyscritobaeus* Perkins. Specimens collected during field studies in California and reevaluation of specimens determined as *G. myrmecophilum* in Mexico reveal that *G. aetherium* is adventive in North America.

Keywords

Gryon, taxonomy, bagrada bug

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Introduction

Bagrada bug, *Bagrada hilaris* (Burmeister) (Hemiptera, Pentatomidae), is an agriculturally destructive pest that has invaded North and South America (Palumbo and Natwick 2010; Bundy et al. 2012; Reed et al. 2013; Sánchez-Peña 2014; Faúndez et al. 2016; Palumbo et al. 2016). It is a pest of several brassicaceous crops and ornamental plants (Palumbo and Natwick 2010; Reed et al. 2013) and young seedlings are particularly vulnerable to feeding damage (Huang et al. 2014). Current control practices rely mostly on conventional insecticides which lead to increased production costs and negative impacts on natural enemies and human health (Stark and Banks 2003). Initial surveys in northern and central California, where most of the nation's brassicaceous crops are grown, found that parasitoids attacked far less than 1% of sentinel eggs that were deployed (B. Hogg, unpublished data). The unique oviposition behavior of *B. hilaris*, the only pentatomid species known to bury its eggs in the soil (Taylor et al. 2014), is a likely factor in limiting the efficacy of natural enemies in newly invaded regions.

Economic consequences caused by the bagrada bug were at times severe, with 53 certified organic cole crop farms in California reporting losses of $25,000 to $100,000 from bagrada bug in 2014–2015, resulting in total annual losses of $1.3 to 5.3 million for these farms alone (California Certified Organic Farmers, personal communication). This prompted the initiation of a biological control program that imported egg parasitoids from Pakistan (Mahmood et al. 2015), the most likely origin of the invasive *B. hilaris* population in the United States (Sforza et al. 2017), into quarantine facilities for host range testing. Two of the most promising species were egg-parasitoid wasps in the family Scelionidae: *Trissolcus hyalinipennis* Rajmohana & Narendran and a species of *Gryon* Haliday. The recent revision of *Trissolcus* Ashmead in the Palearctic region (Talamas et al. 2017a) made identification of the former a straightforward task, demonstrating the value of taxonomic preparedness as discussed by Buffington et al. (2018).

Regarding taxonomic preparedness in *Gryon*, the North America fauna was revised by Masner (1983) but thorough and methodical treatments at the species-level are lacking for most other parts of the world. This created a challenge for identifying the *Gryon* species (*G. aetherium* Talamas) that stood out as a promising classical biocontrol

agent because of its ability to parasitize 25–55% of the eggs laid in the soil in laboratory settings (Tofangsazi et al. 2020; Martel and Sforza 2021). This species was initially identified by the first author as *Gryon gonikopalense* Sharma, based on the proximity of the collecting locality of the holotype (India) to that of the biological control agent (Pakistan), and the apparent congruence of morphology among the specimens examined. However, *G. gonikopalense* was originally described from a single specimen (Figures 77–78), precluding evaluation of intraspecific variability or characters that are obscured by glue or missing from the holotype specimen (e.g., wings). Martel et al. (2019) mentioned that the name of the biocontrol agent might change as the taxonomy of *Gryon* improved and alerted readers to this possibility. The name *G. gonikopalense* has since been used in Tofangsazi et al. (2020), Martel and Sforza (2021), Hougardy and Hogg (2021) and Martel et al. (2021).

As the project progressed, the morphological similarity between species and the appearance of vast geographical ranges for some *Gryon* species made it clear that this identification needed to be verified with a more intensive analysis that included both molecular data and a broader examination of specimens. The former had the potential to determine if *Gryon* could be separated into morphologically identifiable, monophyletic species groups and so representatives from throughout the genus were analyzed. Some characters that we found to be important for diagnosis were not used by previous workers, thus requiring a fresh examination of primary types to correctly characterize and place species. Given the species richness of *Gryon*, this is a laborious, ongoing task that is essential for advancing its taxonomy. It has required travel on five continents and nearly five years to make a reasonably confident statement about the identity of the parasitoid species in question.

Scelionid parasitoids of *Bagrada hilaris*

Field studies in North America reported seven species of scelionid wasps associated with bagrada bug eggs. Four species of *Trissolcus* were reared in southern California: *Trissolcus basalis* (Wollaston), *Tr. hullensis* (Harrington), *Tr. utahensis* (Ashmead), and the adventive *Tr. hyalinipennis* (Ganjisaffar et al. 2018, 2020). In Mexico, a more diverse assemblage of scelionids was recovered from bagrada bug eggs: *Idris elba* Talamas, *Telenomus podisi* Ashmead, *Tr. basalis*, and a species of *Gryon* that was initially determined by the first author as *G. myrmecophilum* (Ashmead) (Felipe-Victoriano et al. 2019; Lomeli-Flores et al. 2019). However, as Felipe-Victoriano et al. (2019) noted, the COI sequences of specimens reared from bagrada eggs in Mexico were highly divergent from *G. myrmecophilum* collected elsewhere on the continent. We here reevaluate and correct the identifications of the *Gryon* species under consideration as a biological control agent and the specimens reared from bagrada eggs in Mexico. This is done considering multiple sources of evidence that include molecular and morphological analyses of specimens from a broad geographical area, comparison to primary types, evaluation of host-related variability, and crossbreeding experiments conducted by Hogg et al. (2021).

A brief history of *Gryon*

Gryon was erected by Haliday (1833), making it among the earliest genera described in Scelionidae. Two decades later, Förster (1856) described *Acolus* and *Hadronotus* in the same publication. Seven years after this, Motschoulsky (1863) described the monotypic *Muscidea*. Thirteen generic names that are junior synonyms of *Gryon* were described during the 20th century, of which 11 were described between 1908 and 1926 (Table 5). *Hadronotus* Förster remained a valid genus until Masner (1961) treated it as a junior synonym of *Gryon*, stating that the characters provided by Förster (1856) and Maneval (1940) were unreliable for separating the two genera. *Gryon* has since been treated as a polytypic taxon in which numerous species groups have been established to provide some level of subgeneric classification for well over 300 species.

Many taxonomic treatments of *Gryon* have been limited in scope, whereas large-scale syntheses are needed to manage a genus of its size. This situation made it clear that major reassessments of its limits and constituent species were needed, including detailed characterization of historic type specimens. We thus prioritized the examination and imaging of primary types. For species whose type material we have yet to examine, we relied on original descriptions for generic placement. This process revealed that many original descriptions are woefully inadequate, and some are so brief that they can hardly be considered the result of serious taxonomic study. Unfortunately, this phenomenon is not limited to *Gryon* and many taxa in Platygastroidea are plagued by a casual approach to assigning names to species.

Species groups

One of our initial goals was to delimit species groups within *Gryon* to facilitate revisionary projects of more manageable size. This task is beyond the scope of the current treatment. However, we are confident that our phylogenetic analyses provide a significant step toward a subgeneric classification and preliminary examination has revealed numerous morphological characters that warrant further study.

The maximalist approach

We term our approach to the systematics of *G. aetherium* as "maximalist" for a few reasons. First, we employed biological, morphological, and molecular species datasets in the delimitation of this species and experimentally assessed the effect of host species on intraspecific variation. This level of analysis is rarely conducted in the original description of species, and though likely not feasible for many taxa, it is warranted by the the economic and agricultural significance of *G. aetherium*. Second, we have simultaneously made every effort to overcome the "superficial description impediment" sensu Meier et al. (2021) to accelerate and facilitate future work on *Gryon* and *Hadronotus*. To this end, we have established new character systems that are informative at the levels of genus and species and demonstrated the utility of the molecular markers used in our phylogenies. We have made freely avail-

able all data for species that are actively under study, including images of all primary types examined (>150) and images of all *Gryon* and *Hadronotus* species that we sequenced for molecular analyses. Lastly, we use the term "maximalist" because our approach may be considered a counterpoint to the recent "minimalist revision" of Sharkey et al. (2021).

Material and methods

Collections

Specimens on which this work is based are deposited in the following repositories with abbreviations used in the text:

ANIC Australian National Collection of Insects, Canberra, Australia
CASC California Academy of Sciences, San Francisco, California, USA
CDFA California Department of Food and Agriculture, Sacramento, California, USA
CNCI Canadian National Collection of Insects, Ottawa, Canada
EMEC Essig Museum of Entomology, Berkeley, California, USA
FSCA Florida State Collection of Arthropods, Gainesville, Florida, USA
HNHM Hungarian Natural History Museum, Budapest, Hungary
ICIPE International Centre of Insect Physiology and Ecology, Nairobi, Kenya
IEBR Institute of Ecology and Biological Resources, Hanoi, Vietnam
MCSN Museo Civico di Storia Naturale "Giacomo Doria", Genoa, Italy
MFNB Museum für Naturkunde Berlin, Berlin, Germany
MNHN Muséum national d'Histoire naturelle, Paris, France
MZLU Lund Museum of Zoology, Lund, Sweden
NHMW Naturhistorisches Museum Wien, Vienna, Austria
NHM Natural History Museum, London, England
OSUC C.A. Triplehorn Insect Collection, The Ohio State University, Columbus, Ohio, USA
SAMA South Australian Museum, Adelaide, Australian
SAMC Iziko Museums of South Africa, Cape Town, South Africa
SNU College for Agriculture and Life Sciences, Seoul National University, Seoul, South Korea
UASK Ukrainian Academy of Science, Kiev, Ukraine
UCFC University of Central Florida Collection of Arthropods, Orlando, Florida, USA
UCRC Entomological Research Museum, University of California, Riverside, California, USA
USNM National Museum of Natural History, Smithsonian Institution, Washington, DC, USA
ZMMU Zoological Museum, Lomonosov Moscow State University, Moscow, Russia

Table 1. PCR primers used in this study.

Primer	Sequence (5'-3')	Citation
18S-H17F	AAATTACCCACTCCCGGCA	Heraty et al. (2004)
18S-H35R	TGGTGAGGTTTCCCGTGTT	
28S-D23F	GAGAGTTCAAGAGTACGTG	Park and Foighil (2000)
28S-b	TCGGAAGGAACCAGCTACTA	Whiting et al. (1997)
SceWgIF-1	GTAAGTGTCACGGGATGTC	Chen et al. (2021)
SceWgIR-1	TTGACTTCACAGCACCAGT	
LCO1490	GGTCAACAAATCATAAAGATATTGG	Folmer et al. (1994)
HCO2198	TAAACTTCAGGGTGACCAAAAAATCA	Cruaud et al. (2010)
LCO1490puc	TTTCAACWAATCATAAAGATATTGG	
HCO2198puc	TAAACTTCWGGRTGWCCAAARAATCA	
LEP-F1	ATTCAACCAATCATAAAGATAT	Hebert et al. (2004)
LEP-R1 C1-J-1632	TAAACTTCTGGATGTCCAAAAA TGATCAAATTTATAAT	Kambhampati and Smith (1995)
C1-N-2191	CCCGGTAAAATTAAAATATAAACTTC	Simon et al. (1994)

Multilocus phylogeny

Extraction, amplification, and sequencing were performed at the European Biological Control Laboratory (EBCL) and the Florida State Collection of Arthropods (FSCA). Genomic DNA was nondestructively isolated from entire specimens using the Qiagen DNeasy kit (Hilden, Germany) as published in Taekul et al. (2014) with the modifications specified in Sabbatini Peverieri et al. (2018). Vouchers from extractions at EBCL were shipped in absolute ethanol to FSCA for further morphological examination. All residual gDNAs are archived at EBCL and FSCA. Amplification procedures, including thermocycling conditions for COI, 18S rRNA, 28S rRNA, and *Wingless*, were done as described in Talamas et al. (2019) with primers provided in Table 1. Amplicon sequencing and sequence editing were done as described in Talamas et al. (2019).

PCRs targeted four loci: two nuclear ribosomal genes, 18S rRNA (variable region V3-V5) and the 28S rRNA (D2-D3 expansion regions), the nuclear gene *Wingless* (exon), and the mitochondrial 5' end of the cytochrome *c* oxydase subunit I gene (COI), also named the barcode region. These loci were selected for their compatibility with previous datasets examining the relationships of platygastroid species across several taxonomic scales (Murphy et al. 2007; Taekul et al. 2014; Talamas et al. 2019; Chen et al. 2021).

The COI barcode was predominantly amplified using the primers of Folmer et al. (1994) and Hebert et al. (2004). When these did not amplify, we used the primers of Cruaud et al. (2010), Kambhampati and Smith (1995) and Simon et al. (1994).

PCRs utilized the KAPA HiFi HotStart Readymix Kit (Roche Diagnostics) per the manufacturer's protocol in 25 µL reactions (Table 2). Amplicons were purified and prepared for sequencing with BigDye Terminator v.3.1 chemistry (Applied Biosystems). Sequence traces were trimmed in Sequencher 5.4.6. and assembled into contigs. Newly generated sequences were submitted to GenBank and their accession number are presented in Suppl. material 1 (highlighted in blue).

Probaryconus Kieffer was selected as the furthest scelionid outgroup to root the phylogenetic analyses based on the topologies of Chen et al. (2021). Diverse ex-

Table 2. Thermocycle conditions.

Primers	Thermocycle
18S-H17F/18S-H35R	1) 98C/3 min; 35× of steps 2–4: 2) 95C/30 sec; 3) 52C/45 sec; 4) 72C/1 min; 5) 72C/10 min; 4C/∞
28S-D23F/28S-b	1) 98C/3 min; 35× of steps 2–4: 2) 95C/30 sec; 3) 57C/45 sec; 4) 72C/1 min; 5) 72C/10 min; 4C/∞
SceWgIF-1/SceWgIR-1	1) 98C/3 min; 35× of steps 2–4: 2) 95C/30 sec; 3) 60C/30 sec; 4) 72C/1 min; 5) 72C/7 min; 4C/∞
LCO1490/HCO2198; LEP-F1/LEP-R1	1) 98C/3 min; 32× of steps 2–4: 2) 95C/30 sec; 3) 50C/30 sec; 4) 72C/45 sec; 5) 72C/7 min; 4C/∞
LCO1490puc/ HCO2198puc	1) 94C/3 min; 10× of steps 2–4: 2) 94C/30 sec; 3) 48C/1 min; 4) 72C/1 min ; 30× of steps 2–4: 2) 94C/30 sec; 3) 50C/1 min; 4) 72C/1 min; 5) 72C/10 min; 4C/∞
C1-J-1632/C1-N-2191	1) 95C/2 min; 30× of steps 2–4: 2) 98C/20 sec; 3) 40C/30 sec; 4) 72C/ 30 sec; 5) 72C/7 min; 4C/∞

emplar scelionid ingroups were included to place *Gryon* specimens within the context of the family (Suppl. material 1). Individual loci were aligned with MAFFT v.7.394 (Katoh and Standley 2013) using either the E-INS-i (18S, 28S) or L-INS-i (COI, *Wingless*) algorithms. The loci were then concatenated into a supermatrix and maximum likelihood phylogenetic analyses were performed with IQ-TREE v1.6.12 (Nguyen et al. 2015). Eight partitions were originally specified for the concatenated data matrix: one partition for each ribosomal gene (18S, 28S) and one partition for each codon position of COI and *Wingless*. Automated model selection and partition merging was performed with ModelFinder as implemented in IQ-TREE (MFP option; Kalyaanamoorthy et al. 2017), which reduced the number of partitions to seven (Table 3). We estimated branch support in our three analyses with two metrics: (1) the non-parametric bootstrap (Felsenstein 1985), (2) the ultrafast bootstrap in IQ-TREE (Hoang et al. 2018). The same concatenated supermatrix and partition file served as input in each analysis. Non-parametric bootstrap support was estimated from 100 bootstrap replicates and 25 independent tree runs. Ultrafast bootstrap support was estimated from 10,000 bootstrap replicates, with the -bnni flag specified to minimize potential model violations (Hoang et al. 2018a), Maximum parsimony tree searches of the concatenated multigene dataset were conducted in MPBoot (Hoang et al. 2018b) using default parsimony ratchet settings. Maximum parsimony support for nodes was assessed using 10,000 ultrafast bootstraps. The phylogenetic tree presented in Figures 1–3 text is the topology recovered from the IQ-TREE ultrafast bootstrap analysis (best tree from 10 independent runs), with UFBoot, non-parametric bootstrap, and MPBoot values indicated on the branches.

COI barcode analysis

The Barcode of Life Database (BOLD; Ratnasingham and Hebert 2007) was mined for additional *Gryon* sequences. This included all sequences identified as *Gryon* in the database. Each barcode generated during this study was queried to the BOLD identification engine. Hits that were returned with 94% or greater sequence similarity, regardless of the identification-level, were included in further analyses. The mined sequences' corresponding BOLD BINs (Ratnasingham and Hebert 2013) containing specimen images and metadata were then examined to further evaluate their identification as

Table 3. Results of the automated model selection analysis conducted on the loci used for phylogenetic inference.

Partition No.	Locus	Model
1	18S+wgl3	TN+F+R8
2	28S	SYM+R5
3	coi1	GTR+F+R5
4	coi2	TVM+F+I+G4
5	coi3	GTR+F+R7
6	wgl1	SYM+I+G4
7	wgl2	SYM+G4

Gryon (Suppl. material 5). Taxon sampling for COI analyses otherwise followed the scelionid multigene dataset scheme.

Initial COI alignments revealed several indel events across Scelionidae. The COI alignment contained 479 scelionid terminals. DNA sequences were translated into amino acids using the invertebrate mitochondrial translation table and aligned using the default settings of MUSCLE (Edgar 2004) as implemented in MEGAX (Kumar et al. 2018). Amino acids were back-translated to DNA for maximum-likelihood phylogenetic analysis in IQ-TREE v2.0.5 (Minh et al. 2020) on the XSEDE computing cluster as part of the CIPRES Science Gateway (Miller et al. 2010). Model selection was performed using ModelFinder (Kalyaanamoorthy et al. 2017) with a single partition. The best-fit model according to the Bayesian Information Criterion was GTR+F+I+G4. Node support was calculated using 2,000 ultrafast bootstrap replicates (Hoang et al. 2018). Tree files were edited in FigTree v1.4.3 (Rambaut 2012) to aesthetically arrange nodes. Scelionid COI amino acids were manually compared to the helix-loop annotations of the elaterid beetle *Agrypnus murinus* (L.) (GenBank accession KJ963738.1) (Pentinsaari et al. 2016). The location (helix or loop) of amino acid deletions was recorded and scored as a COI phenotype across the dataset.

Phylogenetic placement of *Maruzza* Mineo

While screening sequences for potential contaminants and after conducting the phylogenetic analyses presented in Figures 1–4, one of us (EJT) determined a specimen from Taiwan, originally identified as *Hadronotus*, to be *Maruzza japonica* Mineo (Figures 96–99) using the characters in Mineo (1982a). The only sequence data available for *M. japonica* was COI, which was not included in the COI phylogenetic dataset described above based on its placement in a preliminary phylogenetic analysis that identified it as a potential contaminant. The methods for this analysis follow those of the multi-gene scelionid phylogeny, except that taxon sampling was expanded to include specimens for which only COI sequences were available. Our motivation for reporting the results of this analysis is to propose an initial phylogenetic hypothesis for the placement of *Maruzza* within Platygastroidea and provide evidence that supports its status as a valid genus.

Imaging

Photographs were captured with multiple imaging systems: a Z16 Leica lens with a JVC KY-F75U digital camera using Cartograph and Automontage software; an Olympus BX51 compound microscope with a Canon EOS 70D digital SLR camera; and a Leica DM2500 compound microscope with a Leica DFC425 camera; and a Leica M165 compound microscope with a Leica DFC450 camera. Illumination was achieved with a lighting dome or with LED gooseneck lamps and mylar light dispersers. Images were rendered from Z-stacks with Automontage, Helicon Focus or Zerene Stacker. In some cases, multiple montage images were stitched together in Photoshop to produce larger images at high resolution and magnification.

Dissections for scanning electron microscopy were performed with a minuten probe and forceps. Body parts were mounted to a 12 mm slotted aluminum mounting stub (EMS Cat. #75220) using a carbon adhesive tab (EMS Cat. #77825-12) and sputter coated with approximately 70 nm of gold/palladium using Cressington 108 and Denton IV sputtercoaters. Micrographs were captured using a Hitachi TM3000 Tabletop SEM and a Phenom XL G2 Desktop SEM.

Data deposition and informatics

Results of the phylogenetic analyses and their corresponding sequence matrices and partition files have been deposited in Dryad (https://doi.org/10.5061/dryad.dbrv15f18).

The numbers prefixed with acronyms, e.g., "USNMENT" or "OSUC ", are unique identifiers for the individual specimens (note the blank space after some acronyms). The data associated with CUIDs presented in this study are deposited at mbd-db.osu.edu (MBD). Morphological terms were matched to concepts in the Hymenoptera Anatomy Ontology (Yoder et al. 2010) using the text analyzer function. A table of morphological terms and URI links is provided in Suppl. material 4. The description of *Gryon aetherium* was generated from a matrix in the online program vSysLab (vsyslab.osu.edu) in the format of character: state.

Images of many primary types were made available by the Platygastroidea Planetary Biodiversity Inventory and the photographic catalogs of Talamas et al. (2017b) and Talamas and Pham (2017). For each species in which images are deposited in MBD, formerly the Hymenoptera Online Database (HOL), we provide collecting unit identifiers (CUIDs) that can be entered into the search form at mbd-p.asc.ohio-state.edu. For other images, we provide urls either to zenodo.org, where we have deposited additional images, or links where other collections have made these images available. In cases where colleagues have generously provided images of primary types that were uploaded by the present authors, the contributor is listed in the comment section at zenodo.org.

Character annotations

atc acetabular carina (Figure 62)
ats postacetabular sulcus (Figure 62)
axu axillula (Figures 5, 7–8, 23, 25, 27, 34, 36, 51, 87, 101, 109, 113)

eps episternal foveae (Figure 64)
lpc lateral propodeal carina (Figure 65)
lpS1 lateral pit on S1 (Figures 16, 18)
lpT1 lateral pit on T1 (Figures 15, 23, 25, 27, 31, 34, 37, 80, 87, 104, 108, 113)
mc mesopleural carina (Figures 62, 75–76, 78)
mes mesopleural epicoxal sulcus (Figure 62)
mtpl metapleuron (Figures 23, 25)
oc occipital carina (Figure 60)
ps papillary sensilla (Figure 39, 61, 116)
s seta (Figures 9, 103, 109)
sc sublateral carina on T1 (Figures 15, 104, 108)
sgs subgenual spines (Figures 21, 28, 33, 38, 46, 66, 79, 111, 112, 115)
spf sulcus of propodeal foramen (Figures 63, 65)
T1 metasomal tergite 1 (Figure 109)
vplc ventral mesopleural carina (Figure 62)

Quarantine rearing

To assess intraspecific variability, we examined *G. aetherium* that were reared from multiple pentatomid species during host specificity testing. *Bagrada hilaris*, *Thyanta custator* (Fab.), *Holcostethus abbreviatus* Uhler, *Banasa sordida* (Uhler) and *Euschistus conspersus* Uhler were collected in north-central California (Monterey, Alameda, Solano or Yolo counties) and maintained in laboratory cultures at the USDA-ARS in Albany, CA, under 28–30 °C, 30–40% RH and 16L:8D photoperiod. A laboratory colony of *G. aetherium* was maintained in the USDA-ARS quarantine facility in Albany, California, under 22–27 °C, 40–60% RH and 14L:10D, and host specificity tests were conducted in quarantine under the same conditions. Tests followed a no-choice design, whereby individual parasitoids were exposed to one species of pentatomid egg in glass vials. Clusters of 10–15 fresh pentatomid eggs (<24 h old) were glued onto strips of card stock (20 × 60 mm) using Elmer's Glue-All (Elmer's Products Inc., Westerville, OH) and placed in glass vials (25 mm diameter × 95mm high), and one 24- to 48-hour-old, mated female parasitoid was then released into each vial and removed after 24 hours. At least one vial containing *B. hilaris* eggs was also exposed to parasitoids, when possible, to compare the suitability of non-target pentatomids and *B. hilaris* to the parasitoids. Eggs were then monitored, and numbers of parasitized eggs and emerging pentatomids and parasitoids were recorded. Unhatched eggs were then dissected after ~30 days to record numbers of parasitoid larvae that failed to complete development.

Results

Molecular systematics

We used multiple genetic loci and extensive taxon sampling within Platygastroidea to infer the placement of *Gryon aetherium*. The concatenated alignment consisted of 194

taxa, 2,706 sites (base pairs and gaps), and 4.3% missing data. Eighty-one (41%) of the 194 taxa were determined as *Gryon*. Three independent phylogenetic analyses were performed on the alignment that differed by the type of branch support metric (ultrafast bootstrap, non-parametric bootstrap) or tree search strategy (maximum-likelihood, parsimony) employed (Figures 1–3). In all analyses, several clades were recovered that corroborate the results of prior phylogenetic studies on Scelionidae (Taekul et al. 2014; Chen et al. 2021): (1) the basal position of *Neoscelio* Dodd (100% UFBS/NPBS); (2) the polyphyly of the subfamily Scelioninae; (3) the monophyly of the tribe Scelionini (65% UFBS, 33% NPBS); (4) the monophyly of Teleasinae (>95% UFBS/NPBS); and (5) the monophyly of Telenominae *sensu* Taekul et al. (2014) (100% UFBS/NPBS).

The taxa initially determined as belonging to *Gryon* were recovered as a polyphyletic assemblage composed of two clades. Clade A, with 35 taxa, forms a maximally supported (99–100% support) terminal cluster of species that is sister to a weakly supported (76% UFBS, 17% NPBS) clade of spider-egg parasitoids (*Idris* Förster, *Ceratobaeus* Ashmead) (Figure 2). We recognize the taxa in clade A as *Hadronotus*, which we remove from synonymy with *Gryon*. Clade B is composed of 51 taxa and forms a maximally supported (99–100% support) group sister to *Dyscritobaeus* Perkins (97% UFBS, 92% NPBS). Within this clade, the three specimens of *G. aetherium* sp. n. clustered together at maximum support (100%), as a clade basal to *Gryon* specimens from California (USA), Myanmar, and South Africa (Figure 3).

COI barcoding

Sequencing efforts generated 124 new COI barcodes. Annotation of COI amino acids demonstrated that at least four, possibly six, indel phenotypes were present in the scelionid dataset (Table 4, Suppl. material 2). All scelionids analyzed displayed a three amino acid deletion in loop 3, with the single exception of *Platyscelidris fossorius* Johnson & Musetti, which contained a two amino acid deletion in loop 3 (Table 4). The simplest phenotype (present in 43 genera) has a three amino acid deletion in loop 3 with no other detected deletions. This phenotype is present in *Gryon* and *Maruzza* (Table 4). The dataset contained eight *Breviscelio* Sundholm (=*Gryon*) barcodes, two of which spanned the entirety of the annotated *Agrypnus murinus* sequence. The longest two *Breviscelio* sequences had an additional single amino acid deletion present in loop 1 that was not detected in any other of the analyzed genera (Table 4). Another group of COI phenotypes contained additional amino acid deletions in loop 4. The genera *Acanthoscelio* Ashmead, *Baryconus* Förster, *Gryonoides* Dodd, Teleasinae gen. sp., and *Trimorus* Förster displayed single amino acid deletions in loop 4. *Gryonoides* sp. (OSUC 627839) had three amino acids deleted from loop 4, while the other two available *Gryonoides* COI sequences (data not shown in Suppl. material 2) contained only one deletion. A group of 13 genera, including *Hadronotus*, had a two amino acid deletion present in loop 4 (Table 4).

COI barcoding of *G. aetherium* from Mexico, California, and the quarantined colony collected from Pakistan revealed two haplotypes, differing by two synonymous substitutions. One of the haplotypes is a 100% match to two specimens, previously de-

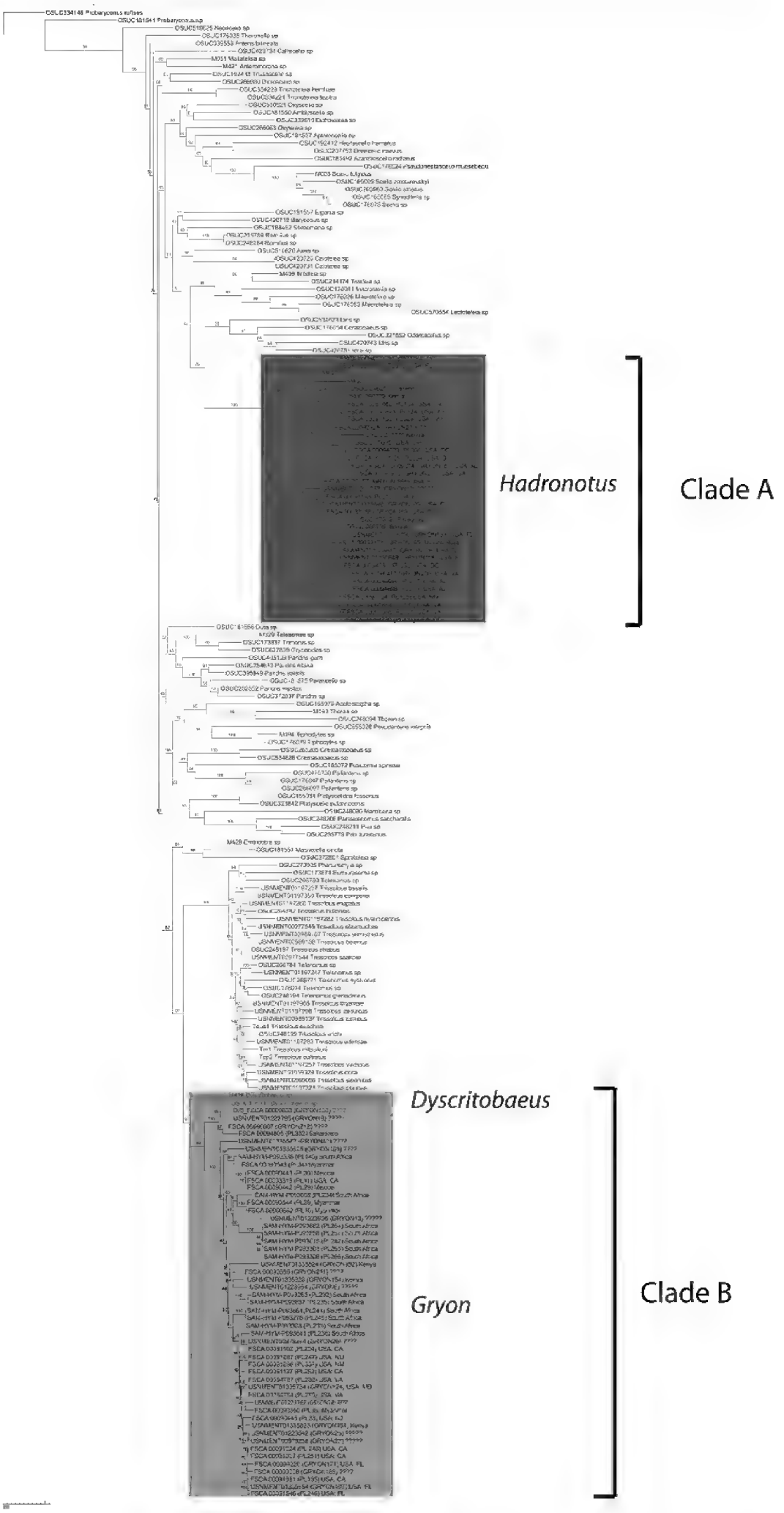


Figure 1. Best tree from the multi-gene, maximum likelihood phylogenetic analysis of Scelionidae conducted in IQ-TREE. Branch support values were generated from 10,000 ultrafast bootstrap replicates and are indicated above branches. The positions of *Hadronotus* (Clade A), *Gryon* (Clade B), and *Dyscritobaeus* (Clade B) are indicated in green, blue, and red, respectively.

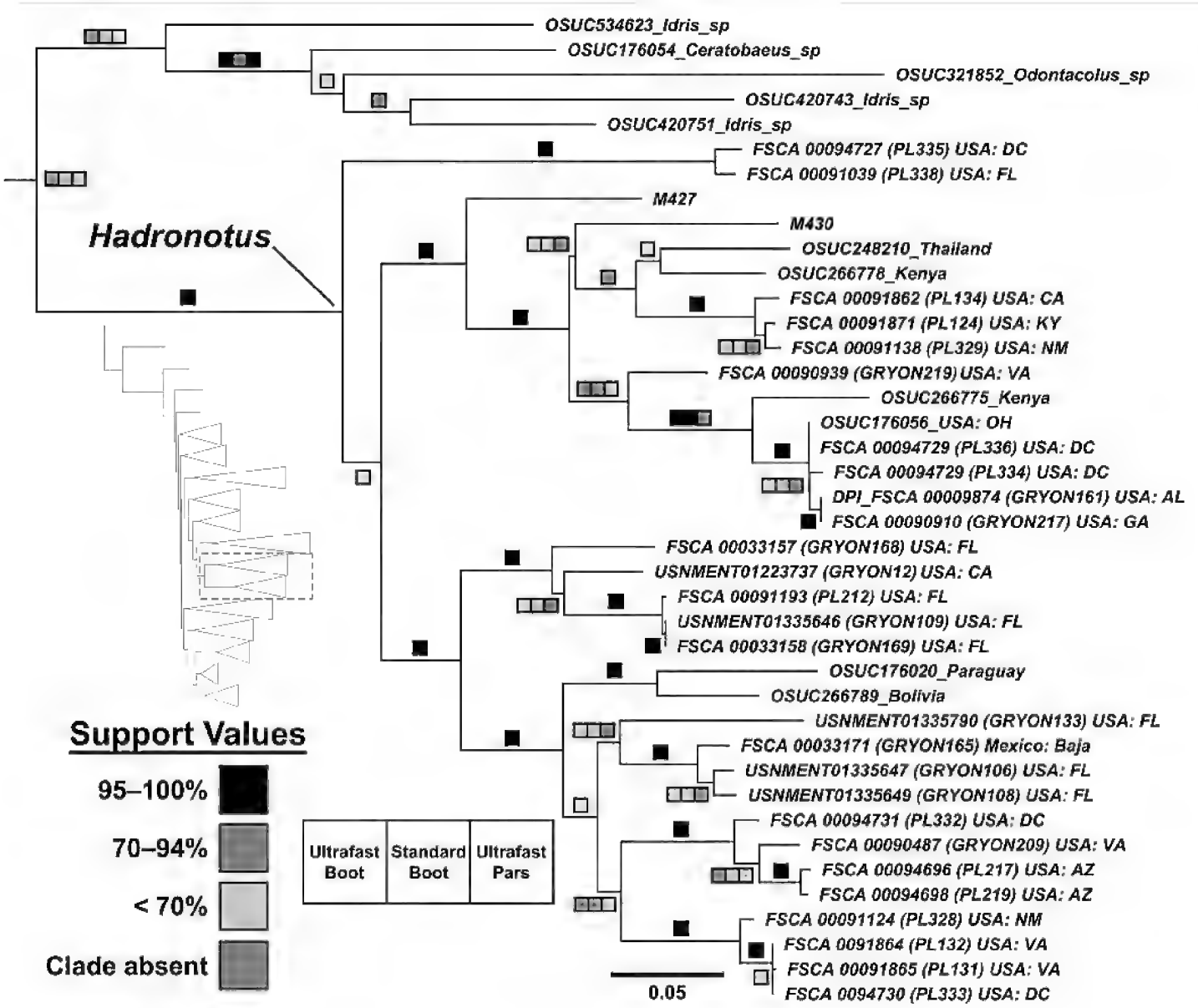


Figure 2. Position and phylogenetic relationships of *Hadronotus* relative to other Scelionidae based on the topology depicted in Figure 1. Colored boxes above branches correspond to the level of support obtained for that branch based on the support metric. Branches annotated with a single box received equal levels of support in all analyses. The scale bar indicates the expected number of substitutions per site.

termined as *G. myrmecophilum* from Coahuila, Mexico (MK720831 and MK720832). These specimens (FSCA 00090442, FSCA 00090443) were misidentified and are *G. aetherium*. BOLD queries of *G. aetherium* barcodes yielded greater than 99% matches to 41 additional public sequences in BIN BOLD:ACF7890. The sequence hits were from Pakistan, Egypt, and South Africa and are identified as Scelioninae. Examination of the three images associated with BIN BOLD:ACF7890 revealed that they are consistent with *G. aetherium*. These additional sequences suggest several more COI haplotypes of *G. aetherium*, all with about 99% sequence similarity to each other. Based on the overall sequence similarity, specimen images, and specimen locality data we consider that BIN BOLD:ACF7890 corresponds to *G. aetherium*, suggesting that the species has a wide distribution. The next nearest cluster of sequences to *G. aetherium* in BOLD are private and identified only as Platygastridae from Israel and Lebanon.

Maximum-likelihood tree searches of the scelionid COI barcode dataset recovered a bootstrap consensus tree of log-likelihood -39550.451 (Figure 4). The tree topology

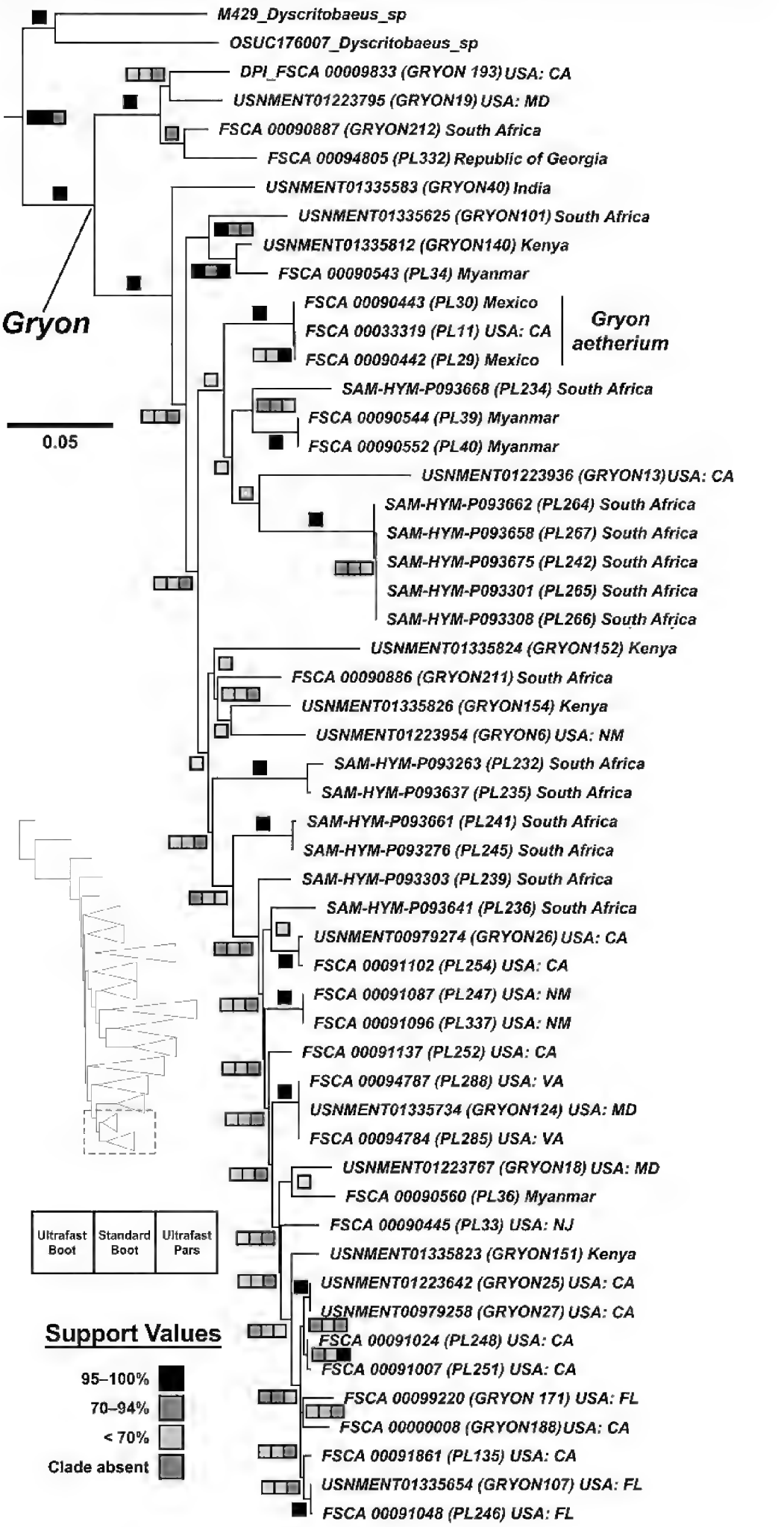


Figure 3. Position and phylogenetic relationships of *Gryon* relative to other Scelionidae based on the topology depicted in Figure 1. Colored boxes above branches correspond to the level of support obtained for that branch based on the support metric. Branches annotated with a single box received equal levels of support in all analyses. The scale bar indicates the expected number of substitutions per site.

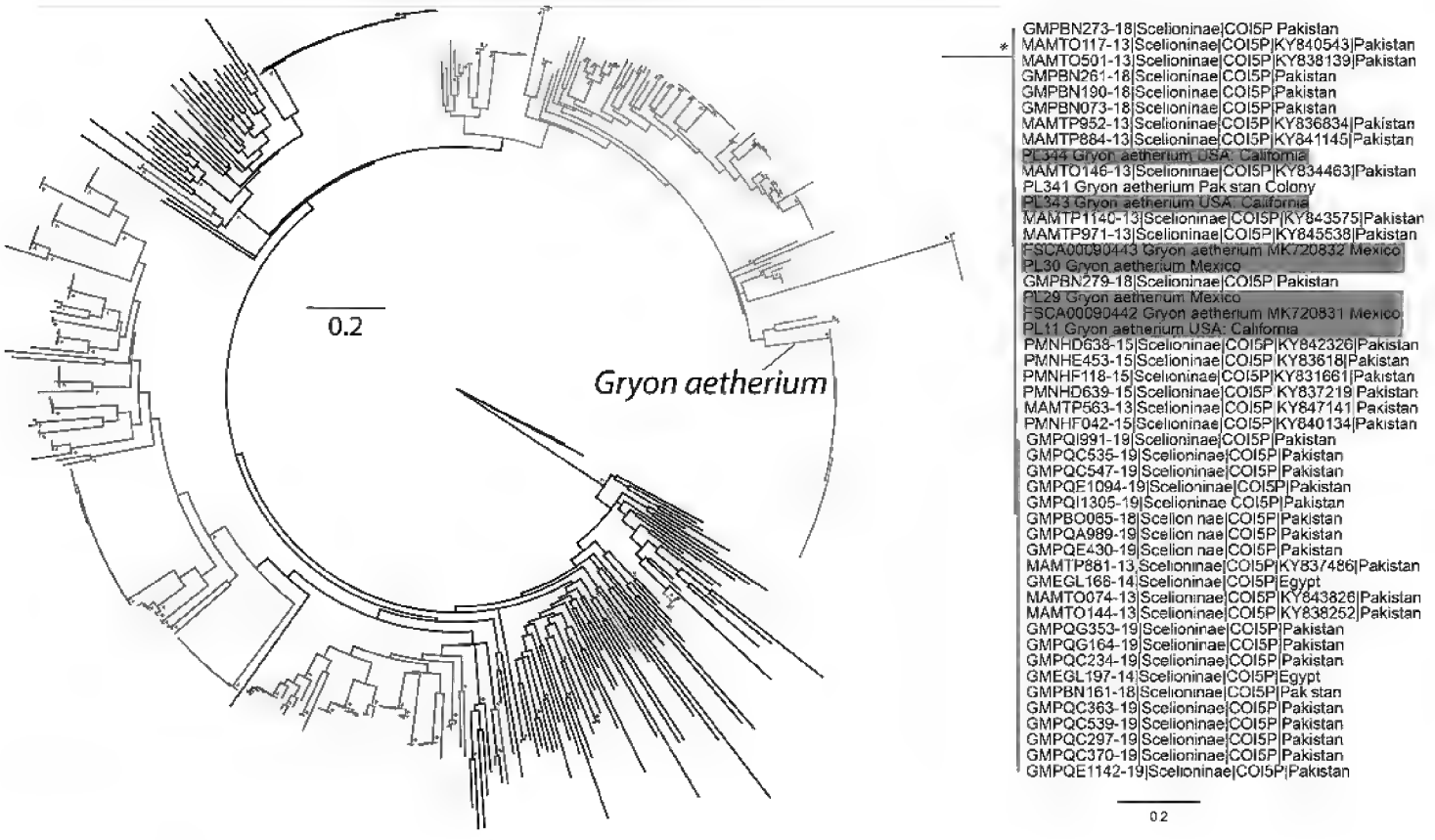


Figure 4. Phylogenetic relationships of Scelionidae based on a maximum likelihood analysis of 479 COI sequences. Branches in blue and red indicate *Hadronotus* and *Gryon*, respectively. Terminals belonging to *G. aetherium* are shown to the right of the phylogenetic tree. Terminals highlighted in yellow correspond to adventive *G. aetherium* specimens collected in Mexico and California. Scale bars indicate the expected number of substitutions per site.

contains 89 nodes with strong support (>95% UFBS), with most strongly supported nodes corresponding to terminal clusters with some interesting exceptions (Figure 4). A *Gryon aetherium* cluster was recovered with 100% support. This terminal cluster is nested within a larger group of sequences with marginal support (92% UFBS) identified as *Gryon* or predicted to be *Gryon* from our datamining procedure. The large *Gryon* clade was recovered as sister (with very weak support) to a strongly supported (100% UFBS) clade comprising *Telenomus* Haliday, *Phanuromyia* Dodd, *Trissolcus*, *Gryonoides*, and two *Gryon*. *Hadronotus* sequences, and those predicted to be *Hadronotus* from our datamining procedure, were more variably placed in the topology. One clade of *Hadronotus* was recovered as sister to *Fusicornia* Risbec with weak support. Internal to this node, support becomes stronger (88% UFBS and 98% UFBS) (Suppl. material 3). The remaining *Hadronotus* fell into a weakly supported clade (54% UFBS) that included *Idris*, *Ceratobaeus*, *Odontacolus* Kieffer and *Thoronella* Masner (Suppl. material 3).

Character discussion

Axillula

The scutellar-axillar complex is a rich source of characters that have yet to be fully exploited in the taxonomy of Platygastroidea. Striation within the area delimited by the

Table 4. COI amino acid phenotypes of Scelionidae. Taxa are listed and colored according to phenotype. *Gryon* and *Hadronotus* are highlighted in blue.

Genus	No. Seq.	Helix 1	Loop 1	Helix 2	Loop 2	Helix 3	Loop 3	Helix 4	Loop 4	Helix 5	Loop 5	Helix 6
Acolomorpha	1	–	–	–	No	No	3 AA deletion	No	No	No	No	No
Amblyscelio	1	–	–	–	No	No	3 AA deletion	No	No	No	No	No
Anteromorpha	1	–	–	–	–	No	3 AA deletion	No	No	No	No	No
Apteroscelio	1	–	–	–	No	No	3 AA deletion	No	No	No	No	No
Calliscelio	1	–	No	No	No	No	3 AA deletion	No	No	No	No	No
Calotelea	2	–	–	–	No	No	3 AA deletion	No	No	No	No	No
Ceratobaeus	1	–	–	–	No	No	3 AA deletion	No	No	No	No	No
Cremastobaeus	2	–	No	No	No	No	3 AA deletion	No	No	No	No	No
Dicroscelio	1	–	No	No	No	No	3 AA deletion	No	No	No	No	No
Duta	1	–	–	–	–	No	3 AA deletion	No	No	No	No	No
Dyscritobaeus	2	–	–	–	No	No	3 AA deletion	No	No	No	No	No
Elgonia	1	–	–	–	–	No	3 AA deletion	No	No	No	No	No
Embidobia	1	–	–	–	–	No	3 AA deletion	No	No	No	No	No
Fusicornia	1	–	No	No	No	No	3 AA deletion	No	No	No	No	No
Gryon	157	No	No	No	No	No	3 AA deletion	No	No	No	No	No
Heptascelio	1	–	–	–	No	No	3 AA deletion	No	No	No	No	No
Idris	3	–	–	–	No	No	3 AA deletion	No	No	No	No	No
Leptoteleia	1	–	–	–	No	No	3 AA deletion	No	No	No	No	No
Macroteleia	3	–	–	–	No	No	3 AA deletion	No	No	No	No	No
Mantibaria	1	–	–	–	No	No	3 AA deletion	No	No	No	No	No
Maruzza	1	–	–	No	No	No	3 AA deletion	No	No	No	No	No
Masnerella	1	–	–	–	No	No	3 AA deletion	No	No	No	No	No
Neoscelio	1	–	–	–	No	No	3 AA deletion	No	No	No	No	No
Odontacolus	1	–	–	–	No	No	3 AA deletion	No	No	No	No	No
Oreiscelio	1	–	–	–	No	No	3 AA deletion	No	No	No	No	No
Oxyscelio	1	–	–	–	No	No	3 AA deletion	No	No	No	No	No
Oxyteleia	1	–	–	–	No	No	3 AA deletion	No	No	No	No	No
Parascelio	1	–	–	–	No	No	3 AA deletion	No	No	No	No	No
Paratelenomus	1	–	–	–	No	No	3 AA deletion	No	No	No	No	No
Platyscelio	1	–	–	–	No	No	3 AA deletion	No	No	No	No	No
Probaryconus	2	–	–	–	No	No	3 AA deletion	No	No	No	No	No
Pseudanteris	1	–	–	–	No	No	3 AA deletion	No	No	No	No	No
Pseudoheptascelio	1	–	–	–	No	No	3 AA deletion	No	No	No	No	No
Psilanteris	3	–	–	–	No	No	3 AA deletion	No	No	No	No	No
Psix	2	–	–	–	No	No	3 AA deletion	No	No	No	No	No
Romilius	2	–	No	No	No	No	3 AA deletion	No	No	No	No	No
Scelio	4	–	–	–	No	No	3 AA deletion	No	No	No	No	No
Shreemana	1	–	–	–	–	No	3 AA deletion	No	No	No	No	No
Spiniteleia	1	–	No	No	No	No	3 AA deletion	No	No	No	No	No
Synoditella	1	–	–	–	No	No	3 AA deletion	No	No	No	No	No
Tiphodytes	2	–	–	–	No	No	3 AA deletion	No	No	No	No	No
Trichoteleia	2	No	No	No	No	No	3 AA deletion	No	No	No	No	No
Trissoscelio	1	–	–	–	No	No	3 AA deletion	No	No	No	No	No
Triteleia	2	–	–	–	No	No	3 AA deletion	No	No	No	No	No
(*Gryon*) *Breviscelio*	8	No	1 AA deletion	No	No	No	3 AA deletion	No	No	No	No	No
Acanthoscelio	1	–	–	–	No	No	3 AA deletion	No	1 AA deletion	No	No	No

Genus	No. Seq.	Helix 1	Loop 1	Helix 2	Loop 2	Helix 3	Loop 3	Helix 4	Loop 4	Helix 5	Loop 5	Helix 6
Baryconus	1	–	No	No	No	No	3 AA deletion	No	1 AA deletion	No	No	No
Gryonoides	1	–	No	No	No	No	3 AA deletion	No	3 AA deletion*	No	No	No
Teleasinae gen. sp.	1	–	–	–	–	No	3 AA deletion	No	1 AA deletion	No	No	No
Trimorus	1	–	–	–	No	No	3 AA deletion	No	1 AA deletion	No	No	No
Anteris	1	–	–	–	–	No	3 AA deletion	No	2 AA deletion	No	No	No
Axea	1	–	–	–	No	No	3 AA deletion	No	2 AA deletion	No	No	No
Dichoteleas	1	–	–	–	No	No	3 AA deletion	No	2 AA deletion	No	No	No
Eumicrosoma	1	No	No	No	No	No	3 AA deletion	No	2 AA deletion	No	No	–
Hadronotus	169	No	No	No	No	No	3 AA deletion	No	2 AA deletion	No	No	No
Mallateleia	1	–	–	–	–	No	3 AA deletion	No	2 AA deletion	No	No	No
Paridris	5	–	–	–	No	No	3 AA deletion	No	2 AA deletion	No	No	No
Phanuromyia	1	–	–	–	No	No	3 AA deletion	No	2 AA deletion	No	No	No
Platyscelidris	1	–	–	–	No	No	2 AA deletion**	No	2 AA deletion	No	No	No
Telenomus	43	No	No	No	No	No	3 AA deletion	No	2 AA deletion	No	No	No
Thoron	2	–	–	–	No	No	3 AA deletion	No	2 AA deletion	No	No	No
Thoronella	1	–	–	–	No	No	3 AA deletion	No	2 AA deletion	No	No	No
Trissolcus	22	No	No	No	No	No	3 AA deletion	No	2 AA deletion	No	No	No

**Gryonoides* sp. OSUC 627839 displays a 3 AA deletion in loop 4. Other available *Gryonoides* barcodes contain a single AA deletion in loop 4. ***Platyscelidris fossorius* OSUC 165081 is the only sequence with a 2 AA deletion in loop 3.

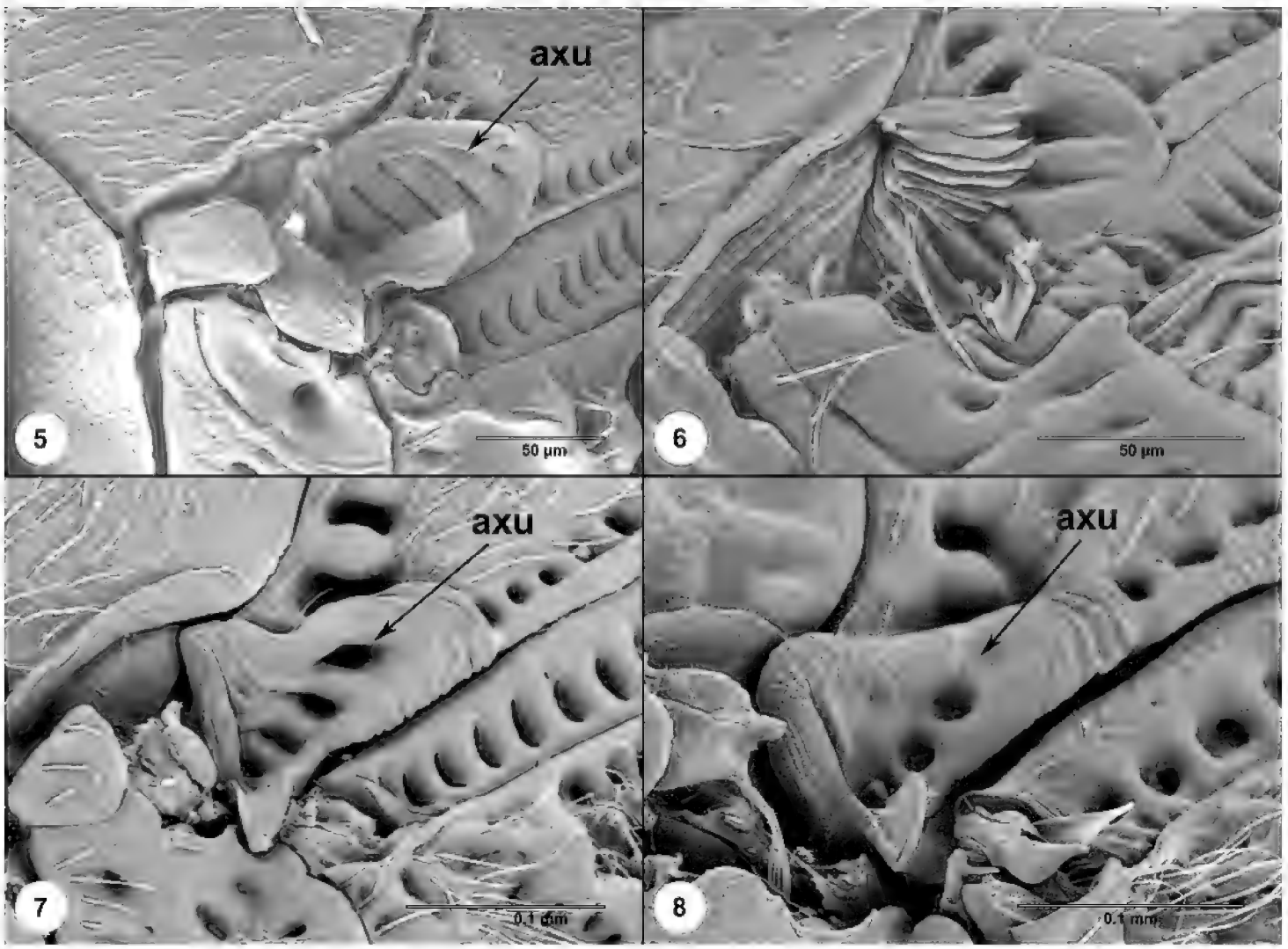
axillar, transaxillar, and axillular carinae can take a variety of forms (Figures 5–8). Figure 6 illustrates this area in *Duta* Nixon where the foveae on the posterior and ventral portions are orthogonal to each other and the anterior portion has a series of flanges. In *Gryon*, the axillula is striate with the striae parallel or nearly so. The striae are oblique relative to the longitudinal axis of the body and oriented from anterodorsal to posteroventral. This is generally a reliable character for *Gryon*, albeit one that is sometimes obscured by the base of the forewing, and we know of two cases in which the striae are largely absent or irregular (see comments sections for *G. moczari* and *G. paradigma*). In *Hadronotus*, the foveae within the axillula can be ovoid or circular (Figures 7–8).

Metapleuron

The metapleuron in *Gryon* has 1–3 setae in the anterodorsal corner and occasionally a single seta in the dorsal metapleural area, but it is otherwise glabrous (Figure 9). In *Hadronotus*, setation is typically present in the foveae of the paracoxal sulcus, the metapleural epicoxal sulcus, and the posterior or posterodorsal portion of the sclerite (Figures 10–12). In many cases, the metapleuron is divided antero-posteriorly by a carina or a change in setation or sculpture (Figures 11–13). For example, in *H. anserculus* (Mineo), a line of sparse setae separates the posterior, smooth portion from the anterior, more rugose portion (Figure 13). In a few cases, such as *H. canus* (Mineo), the entire metapleuron is setose (Figure 14).

Metasomal tergite 1

In *Gryon*, the line of foveae along the anterior margin of T1 terminates laterally at a carina (Figure 15, sc) that is more robust that any adjacent striation; directly

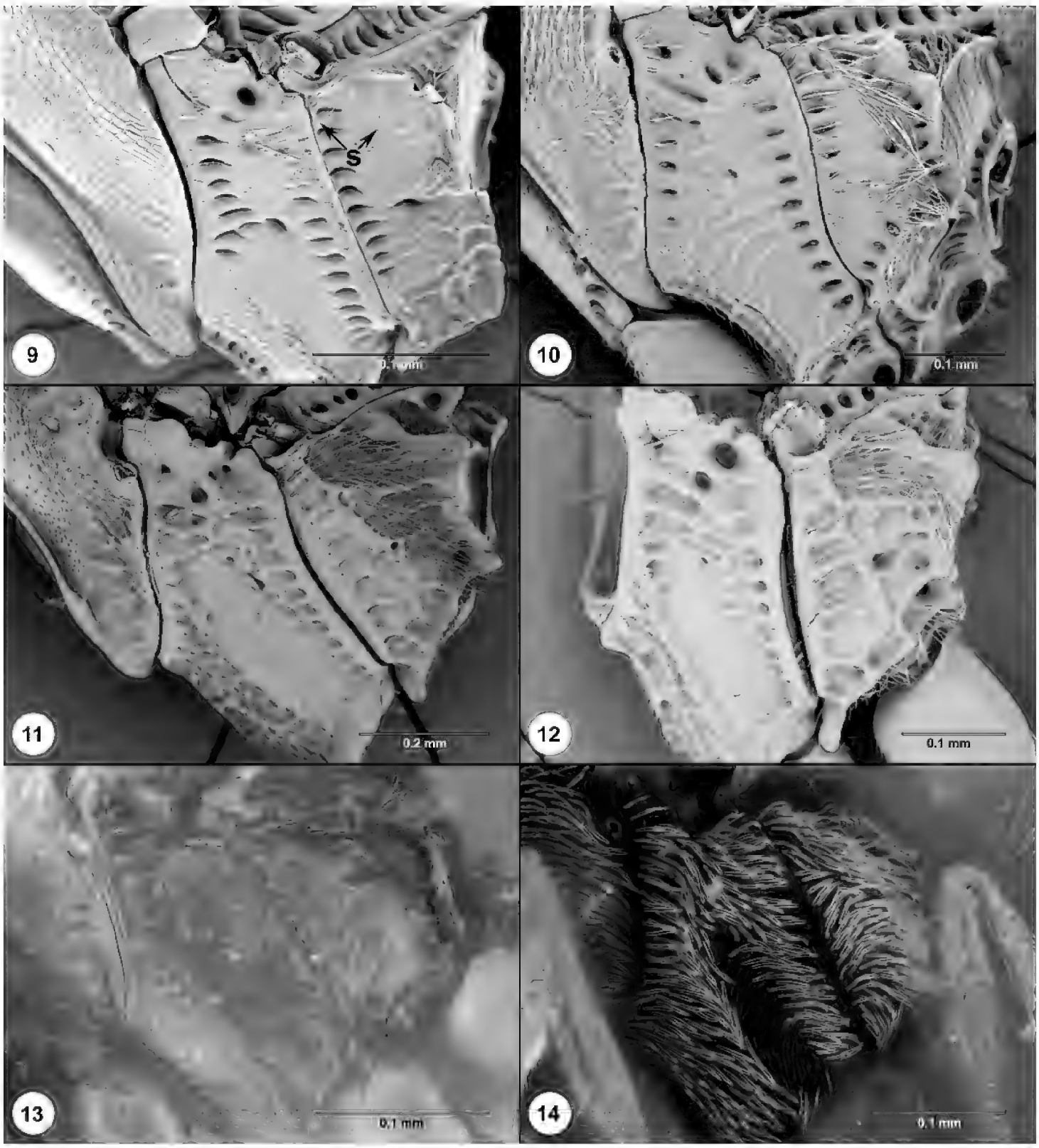


Figures 5–8. Scutellar-axillar complex, lateral view **5** *Gryon aetherium* (USNMENT01109155) **6** *Duta* (USNMENT01109621_2) **7** *Hadronotus hogenakalensis* (DPI_FSCA 00008722) **8** *Hadronotus carinatifrons* (USNMENT01335649).

lateral to this carina is a pit (Figure 15, lpT1). The foveae along the anterior margin are uniform in size and distinctly smaller than the lateral pit. In *Hadronotus*, the foveae along anterior T1 are largest at the midline and decrease in size laterally (Figures 17, 19). In most cases, there is no suggestion of a pronounced carina or lateral pit, but in *H. bicolor* Ashmead, for example, the penultimate fovea on lateral T1 is larger than the fovea directly mesad (Figure 18). However, this does not approximate the form found in *Gryon*. The pattern along anterior S1 in *Gryon aetherium* is essentially identical to that on T1, with a line of uniform, small foveae terminating at a carina, then a large pit (Figure 16, lpS1). However, we do not yet draw any conclusions about S1 in *Gryon* because this sclerite is not easily visible in most specimens and we have dissected and analyzed a relatively small number of species. The presence of a large lateral pit on S1 is more common in Scelionidae and it appears in both *Hadronotus* (Figures 18, 20) and Teleasinae.

Diagnostic summary

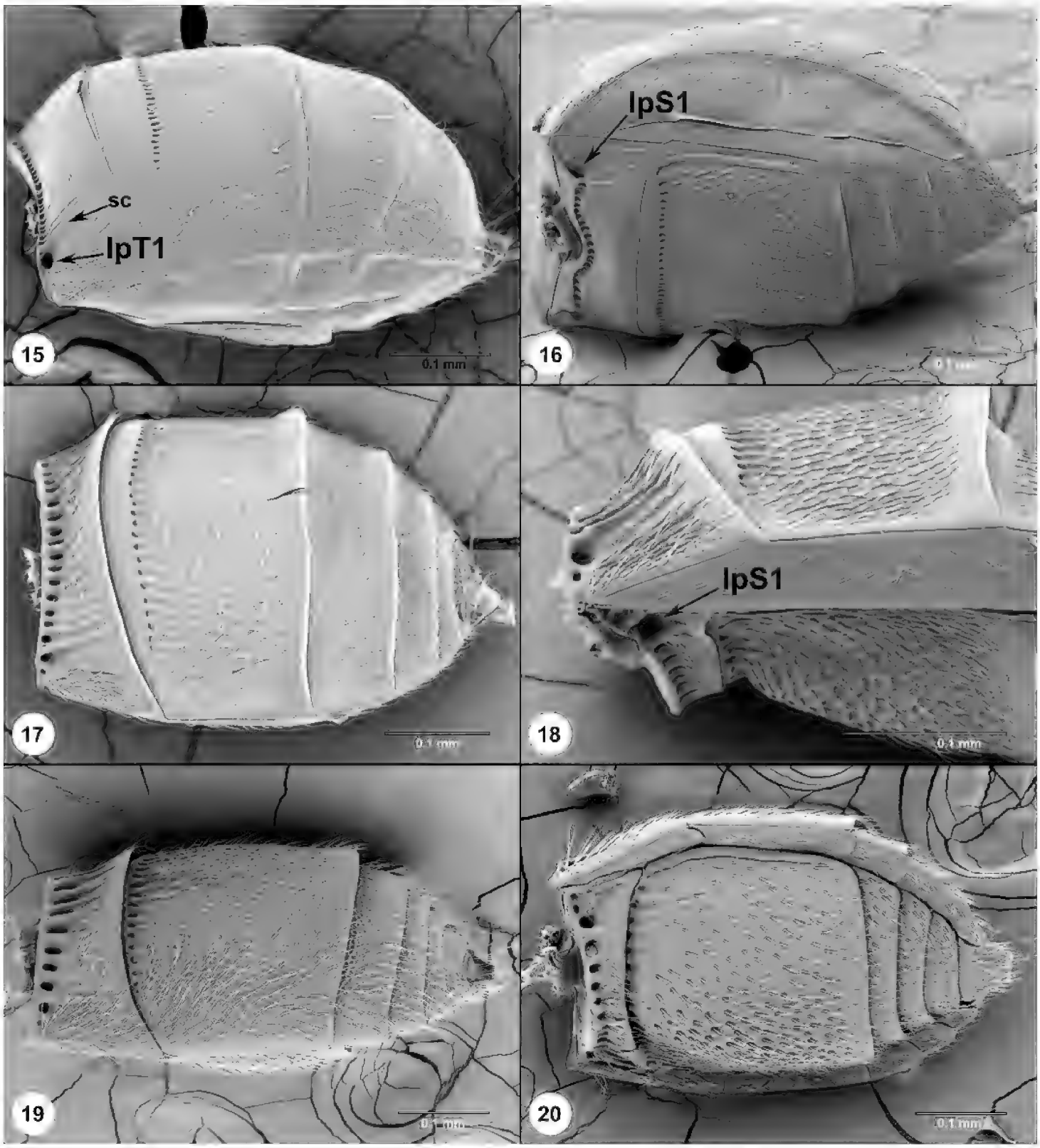
1 Clypeus not projecting ventrally; antennal scrobe with transverse sculpture; metapleuron divided dorsoventrally by a change in sculpture or setation; metapleuron usually setose in posterior portion; hind tibia without subgenual



Figures 9–14. Mesosoma, lateral view **9** *Gryon aetherium* (FSCA 00094874) **10** *Hadronotus hogenakalensis* (DPI_FSCA 00008722) **11** *Hadronotus ater* (FSCA 00094730) **12** *Hadronotus pennsylvanicus* (FSCA 00091081) **13** *Hadronotus anserculus*, holotype female **14** *Hadronotus canus*, holotype female.

spines; foveae along anterior T1 decreasing in size laterally, not bordered laterally by a carina or pit ..... ***Hadronotus*** **Förster**

– Clypeus projecting ventrally, usually with sharp lateral corners; antennal scrobe without transverse sculpture; metapleuron undivided dorsoventrally by a change in sculpture or setation; metapleuron with 1–3 setae in anterodorsal corner, sometimes with a single seta in dorsal metapleural area, otherwise glabrous; hind tibia with subgenual spines; foveae along anterior T1 roughly equal in size, ending in a sublateral carina or pit ..... ***Gryon*** **Haliday**



Figures 15–20. Metasoma **15** *Gryon aetherium* (FSCA 00094873), dorsolateral view **16** *Gryon aetherium* (FSCA 00094873) ventrolateral view **17** *Hadronotus bicolor* (FSCA 00091193), dorsolateral view **18** *Hadronotus bicolor* (FSCA 00091193), lateral view **19** *Hadronotus carinatifrons* (USNMENT01335649), dorsolateral view **20** *Hadronotus carinatifrons*, ventrolateral view.

Images

Links to images of primary or secondary types are provided in the treatment for each species. Table 5 includes these links for primary types of genera and summarizes the rearrangement of generic synonyms in *Gryon* and *Hadronotus*. Table 6 lists the specimens in the molecular analyses that have been photographed, which includes all specimens of *Gryon* and most *Hadronotus*, to further illustrate the characters associated with these

genera and some of the diversity of their constituent species. Images of *Maruzza japonica*, also from the molecular analysis, are presented in Figures 96–99.

Gryon Haliday

Gryon Haliday, 1833: 271 (original description. **Type species:** *Gryon misellum* Haliday, by monotypy, keyed); Walker, 1836: 343 (description); Westwood, 1840: 77 (description); Blanchard, 1840: 289 (junior synonym of *Teleas* Latreille); Brullé, 1846: 619 (description); Förster, 1856: 101, 105 (diagnosis, keyed); Marshall, 1873: 16 (catalog of species of Britain); Walker, 1874: 9 (keyed); Howard, 1886: 172 (keyed); Cresson, 1887: 84 (keyed); Ashmead, 1893: 181, 205 (description, keyed, key to species of U.S. and Canada); Dalla Torre, 1898: 502 (catalog of species); Ashmead, 1900: 327 (list of species of West Indies); Ashmead, 1903: 90 (keyed); Kieffer, 1908: 188, 189 (description, keyed); Brues, 1908: 19, 25, 49 (diagnosis, keyed, list of species); Kieffer, 1910: 91, 92 (description, list of species, keyed); Kieffer, 1912: 109 (description); Kieffer, 1913: 212 (description, taxonomic status, key to species of Europe and Algeria); Dodd, 1914a: 75 (keyed); Kieffer, 1926: 173, 260 (description, keyed, key to species); Morley, 1929: 54 (catalog of species of Britain); Dodd, 1930: 42 (keyed); Nixon, 1936: 115 (taxonomic status, position); Maneval, 1940: 112, 113 (keyed); Fouts, 1948: 92 (keyed); Muesebeck & Walkley, 1951: 356 (citation of type species); Masner, 1961: 158 (synonymy, systematic position, description); Kozlov, 1963a: 354, 357 (description, key to species of USSR, keyed); Kozlov, 1963b: 661, 667 (description, keyed, key to species); Szabó, 1966: 422 (keyed); De Santis, 1967: 225 (catalog of species of Argentina); Safavi, 1968: 418 (parasitized eggs of Scutelleridae keyed); Hellén, 1971: 5, 21 (description, keyed); Kozlov, 1971: 38 (keyed); Kozlov, 1972: 654 (key to new species described); Alayo Dalmau, 1973: 99 (catalog of species of Cuba); Simons, Reardon & Ticehurst, 1974: 15 (keyed); Viggiani & Mineo, 1974: 160, 161 (keyed); Mani & Mukerjee, 1976: 497 (key to new species described); Masner, 1976: 7, 57 (description, synonymy, keyed); Fergusson, 1978: 118 (checklist of species of Britain); Kozlov, 1978: 619 (description, key to species of European USSR); Mineo, 1979b: 91 (diagnosis, key to species parasitizing *Aelia* and *Eurygaster* (Hemiptera: Pentatomidae)); Muesebeck, 1979: 1157 (catalog of species of U.S. and Canada); Masner, 1980: 12, 13 (keyed); Mineo, 1980b: 216 (diagnoses and keys to species of *insulare* and *pubescens* species groups); De Santis, 1980: 311 (catalog of species of Brazil); Mineo, 1981a: 119 (description and key to species of the *muscaeformis* species group); Mani & Sharma, 1982: 152, 191 (description, keyed); Mineo & Villa, 1982b: 175 (taxonomic value of pleural structures, clypeus, and antennal sensilla); Mineo & Villa, 1982a: 134 (taxonomic value of structures on the posterior surface of the head); Sharma, 1982: 336 (key to species of India); Masner, 1983: 126, 127 (description, morphology, division into species groups, key to species of North America, keyed); Mineo, 1983b: 285 (description and key to species of the *pubescens* species group);

Table 5. A summary of the genera treated as junior synonyms of *Gryon* and *Hadronotus* with links to available images of primary types.

Genus	Date	Type species	Images of Type Specimen
Gryon Haliday	1833	*Gryon misellum* Haliday	https://zenodo.org/record/4498847#.YBrybXlOlaQ
Acolus Förster	1856	*Acolus opacus* Thomson	
Plastogryon Kieffer	1908	*Plastogryon foersteri* Kieffer	
Psilacolus Kieffer	1908	*Acolus xanthogaster* Ashmead	USNMENT00989056
Holacolus Kieffer	1912	*Acolus opacus* Thomson	
Plesiobaeus Kieffer	1913	*Plesiobaeus hospes* Kieffer	
Hadronotellus Kieffer	1917	*Hadronotellus pedester* Kieffer	ZMUC 0002
Heterogryon Kieffer	1926	*Plastogryon sagax* Kieffer	
Synteleia Fouts	1927	*Synteleia coracina* Fouts	USNMENT00989057
Eremioscelio Priesner	1951	*Eremioscelio cydnoides* Priesner	USNMENT01059665
Hungarogryon Szabó	1966	*Hungarogryon moczari* Szabó	Hym.Typ.No. 9634, Mus.Budapest
Masneria Szabó	1966	*Hadronotus lymantriae* Masner	
Pannongryon Szabó	1966	*Pannongryon szelenyii* Szabó	https://zenodo.org/record/4521320#.YCGzRnlOlaQ
Sundholmia Szabó	1966	*Sundholmia nitens* Szabó	
Breviscelio Sundholm	1970	*Breviscelio crenatus* Sundholm	https://www.flickr.com/photos/127240649@N08/50616991701/in/photolist-2k7Rjat-2k7Mx3Y-2k7Rj9M-2k7RTii-2k7Rja8/
Exon Masner	1980	*Exon californicum* Masner	
Hadronotus Förster	1856	*Hadronotus exculptus* Förster	https://zenodo.org/record/4504407#.YCGDd3lOlaQ
Muscidea Motschoulsky	1863	*Muscidea pubescens* Motschoulsky	https://zenodo.org/record/4924954#.YOSoF0lKhaQ
Hadronotoides Dodd	1913	*Hadronotus pentatomus* Dodd	SAMA DB 32-001664
Platyteleia Dodd	1913	*Platyteleia latipennis* Dodd	SAMA I.1396
Telenomoides Dodd	1913	*Telenomoides flavipes* Dodd	https://zenodo.org/record/5188097#.YRUi0MpKhaQ
Notilena Brèthes	1913	*Notilena gallardoi* Brèthes	
Austroscelio Dodd	1914	*Sparasion nigricoxa* Dodd	SAMA DB 32-001667
Hadrophanurus Kieffer	1926	*Telenomus pennsylvanicus* Ashmead	https://zenodo.org/record/4520251#.YCGBzXlOlaQ

Mineo, 1983c: 546, 551 (descriptions and keys to species of the *insulare* and *oculatum* species groups); Mineo, 1983a: 12 (description and key to species of the *charon* species group); Galloway & Austin, 1984: 6, 78 (diagnosis, synonymy, list of species described from Australia, keyed); Mineo & Caleca, 1987b: 41 (diagnoses of the *misellum*, *artum*, *austrafricanum* and *hospes* species groups; key to species of the *artum* group); Kozlov & Kononova, 1989: 78 (key to species of the USSR); Kozlov & Kononova, 1990: 96, 265, 266 (description, division into species groups, key to species of Palearctic, keyed); Caleca, 1990a: 116 (description, key to species of *pentatomum* group); Mineo, 1990a: 171, 174, 180, 182 (description of *artum*, *muscaeforme*, *myrmecophilum*, *oculatum*, *pubescens* groups); Mineo, 1990b: 49, 52 (description of *hiberus*, *leptocorisae* species groups); Mineo, 1990c: 90 (description of *letus* group, key to species of *letus* group); Mineo, 1991: 1, 2, 7, 9, 10, 12 (description of *aculum*, *acuteangulatum*, *aureum*, *cydnoide*, *hungaricum*, *introversum* species groups, synonymy, key to species of *hungaricum* group); Johnson, 1992: 374 (cataloged, catalog of world species); Mineo & Caleca, 1994: 114, 116, 121, 127 (designation of *hirsuticolum* group, *fulviventre* subgroup of *muscaeforme* group, *subfasciatum* group, *lymantriae* group, key to species of *lymantriae* group); Kononova, 1995: 62, 81 (keyed, diagnosis, key to species of Russian Far East); Austin

Table 6. List of specimens from the molecular analysis that have been photographed. It includes all specimens of *Gryon* and representatives for each species of *Hadronotus*.

Taxon	CUID	Link to images
Gryon sp.	USNMENT01335610	https://zenodo.org/record/4558207#.YN974ElKhaQ
	USNMENT01335583	https://zenodo.org/record/4558210#.YN98DklKhaQ
	SAM-HYM-P093661	https://zenodo.org/record/4558205#.YN98NElKhaQ
	SAM-HYM-P093276	https://zenodo.org/record/4558203#.YN98PUlKhaQ
Gryon myrmecophilum	USNMENT01335734	https://zenodo.org/record/4558198#.YN98W0lKhaQ
	USNMENT01335823	https://zenodo.org/record/4558187#.YN98eUlKhaQ
	USNMENT01335654	https://zenodo.org/record/4558181#.YN98jUlKhaQ
	USNMENT01335597	https://zenodo.org/record/4558177#.YN98n0lKhaQ
	USNMENT01223867	https://zenodo.org/record/4558173#.YN98sUlKhaQ
	USNMENT01223767	https://zenodo.org/record/4558165#.YN98xUlKhaQ
	USNMENT01223642	https://zenodo.org/record/4558159#.YN985ElKhaQ
	USNMENT00979274	https://zenodo.org/record/4558153#.YN98-ElKhaQ
	USNMENT00979258	https://zenodo.org/record/4558145#.YN99DElKhaQ
	SAM-HYM-P093315	https://zenodo.org/record/4558143#.YN99IklKhaQ
	SAM-HYM-P093303	https://zenodo.org/record/4558141#.YN99N0lKhaQ
	FSCA 00094787	https://zenodo.org/record/4558138#.YN99SklKhaQ
	FSCA 00094784	https://zenodo.org/record/4558120#.YN99e0lKhaQ
	FSCA 00091861	https://zenodo.org/record/4558116#.YN99jklKhaQ
	FSCA 00091137	https://zenodo.org/record/4558108#.YN99zUlKhaQ
	FSCA 00091102	https://zenodo.org/record/4558101#.YN996ElKhaQ
	FSCA 00091067	https://zenodo.org/record/4558093#.YN9-A0lKhaQ
	FSCA 00091048	https://zenodo.org/record/4558089#.YN9-F0lKhaQ
	FSCA 00091024	https://zenodo.org/record/4558084#.YN9-bUlKhaQ
	FSCA 00090560	https://zenodo.org/record/4558078#.YN9-dElKhaQ
	FSCA 00090445	https://zenodo.org/record/4558072#.YN9-fElKhaQ
	FSCA 00033220	https://zenodo.org/record/4558056#.YN9-VElKhaQ
	FSCA 00000032	https://zenodo.org/record/4558051#.YN9-hklKhaQ
	FSCA 00000008	https://zenodo.org/record/4558039#.YN9-mElKhaQ
Gryon sp.	USNMENT01335826	https://zenodo.org/record/4558015#.YN9-rElKhaQ
	USNMENT01335596	https://zenodo.org/record/4558011#.YN9-wklKhaQ
	USNMENT01223954	https://zenodo.org/record/4557989#.YN9-1UlKhaQ
	SAM-HYM-P093637	https://zenodo.org/record/4557969#.YN9-50lKhaQ
	SAM-HYM-P093263	https://zenodo.org/record/4557961#.YN9_DUlKhaQ
	FSCA 00090886	https://zenodo.org/record/4557955#.YN9_H0lKhaQ
	USNMENT01335595	https://zenodo.org/record/4557944#.YN9_PElKhaQ
	SAM-HYM-P093641	https://zenodo.org/record/4557938#.YN9_UklKhaQ
	USNMENT01335824	https://zenodo.org/record/4557928#.YN9_ZUlKhaQ
	FSCA 00033267	https://zenodo.org/record/4557917#.YN9_eElKhaQ
	USNMENT01335812	https://zenodo.org/record/4557913#.YN9_mUlKhaQ
	USNMENT01335625	https://zenodo.org/record/4557902#.YN9_t0lKhaQ
	FSCA 00090543	https://zenodo.org/record/4557899#.YN9_yklKhaQ
	USNMENT01223795	https://zenodo.org/record/4557892#.YN9_30lKhaQ
	USNMENT01223656	https://zenodo.org/record/4557832#.YN-AxUlKhaQ
	FSCA 00090887	https://zenodo.org/record/4557820#.YN-A10lKhaQ
	DPI_FSCA 00009833	https://zenodo.org/record/4557799#.YN-A4UlKhaQ
Gryon crenatum	SAM-HYM-P093675	https://zenodo.org/record/4557773#.YN-A9UlKhaQ
	SAM-HYM-P093658	https://zenodo.org/record/4557739#.YN-BWUlKhaQ
	SAM-HYM-P093308	https://zenodo.org/record/4557727#.YN-BaklKhaQ
Hadronotus sp.	FSCA 00094689	https://zenodo.org/record/5055893#.YORbJjOSmM8
	SAM-HYM-P093286A	https://zenodo.org/record/5055622#.YORbezOSmM8
Hadronotus obesus	DPI_FSCA 00009874	https://zenodo.org/record/5055577#.YORbqTOSmM8
Hadronotus sp.	SAM-HYM-P093613	https://zenodo.org/record/5055533#.YORb2TOSmM8
Hadronotus pennsylvanicus	FSCA 00033171	https://zenodo.org/record/5055465#.YORb_DOSmM8
Hadronotus sp.	FSCA 00094681	https://zenodo.org/record/5047752#.YORcIzOSmM8

Taxon	CUID	Link to images
Hadronotus radicularis	FSCA 00091862	https://zenodo.org/record/5047719#.YORcQzOSmM8
Hadronotus sp.	FSCA 00094687	https://zenodo.org/record/5080975#.YOYIWOhKg2w
	FSCA 00094692	https://zenodo.org/record/5080835#.YOYKsOhKg2w
Hadronotus pennsylvanicus	FSCA 00094782	https://zenodo.org/record/5081043#.YOYODOhKg2w
Hadronotus sp.	SAM-HYM-P093638	https://zenodo.org/record/5086004#.YOhpzzOSmM8
	USNMENT01223737	https://zenodo.org/record/5085986#.YOhqNTOSmM8
	SAM-HYM-P093243	https://zenodo.org/record/5086109#.YOhrgTOSmM8
	SAM-HYM-P093622	https://zenodo.org/record/5086454#.YOh3-ElKhaQ
	SAM-HYM-P093679	https://zenodo.org/record/5086600#.YOh6JElKhaQ
Hadronotus anasae	USNMENT01335790	https://zenodo.org/record/5093270#.YOyFIklKhaQ
Hadronotus atrum	FSCA 00094730	https://zenodo.org/record/5093412#.YOyFEUlKhaQ
Hadronotus carinatifrons	USNMENT01335649	https://zenodo.org/record/5093598#.YOyE8UlKhaQ
Hadronotus bicolor	FSCA 00091193	https://zenodo.org/record/5093580#.YOyFAUlKhaQ
Hadronotus leptocorisae	FSCA 00090459	https://zenodo.org/record/5093611#.YOyE3UlKhaQ
Hadronotus rugiceps	FSCA 00094731	https://zenodo.org/record/5093642#.YOyH_0lKhaQ

& Field, 1997: 36, 68 (structure of ovipositor system, discussion of phylogenetic relationships); Lê, 2000: 32, 95 (keyed, description, key to species of Vietnam); Kononova & Petrov, 2001: 1468 (description); Kononova & Petrov, 2002: 53 (key to species of Palearctic); Loiácono & Margaría, 2002: 557 (catalog of Brazilian species); Rajmohana K., 2006: 115, 123 (description, keyed); Fabritius & Popovici, 2007: 11, 13, 14, 26, 29, 63 (description, key to Romanian species, key to species related to *Gryon longiabdominalis* and *buhli*, keyed); Kononova & Kozlov, 2008: 25, 321, 322 (description, keyed, key to species of Palearctic region); Popovici & Johnson, 2012: 382 (description of internal genitalia); Rajmohana, 2014: 8, 33 (description, keyed); Talamas & Buffington, 2015: 21 (fossil in Dominican amber).

Comments. The lectotype and paralectotype specimens of *G. misellum* Haliday are in excellent condition considering their age (~190 years old) and these specimens display all the diagnostic characters that we associate with the genus (Figures 21–25).

Acolus Förster, 1856: 100, 102 (original description. Type species: *Acolus opacus* Thomson, designated by Ashmead (1903), keyed. Synonymized by Masner (1961)); Thomson, 1859: 417, 422 (description, keyed); Walker, 1874: 9 (keyed); Howard, 1886: 172 (keyed); Cresson, 1887: 83, 313 (keyed, catalog of species of U.S. and Canada); Ashmead, 1893: 167, 168, 174 (description, keyed); Dalla Torre, 1898: 510 (catalog of species); Ashmead, 1903: 88, 89 (keyed); Kieffer, 1908: 179, 180 (description, key to species, keyed); Brues, 1908: 14, 15, 16, 47 (diagnosis, keyed, list of species); Kieffer, 1910: 100, 101 (description, list of species, keyed); Kieffer, 1912: 89, 92 (description, key to species of Europe and Algeria); Kieffer, 1912: 55 (key to species of Seychelles); Dodd, 1914a: 58, 70 (key to species of Australia, keyed); Brues, 1916: 542 (keyed); Kieffer, 1926: 133, 156 (description, keyed, key to species); Jansson, 1939: 173 (keyed); Maneval, 1940: 111 (keyed); Muesebeck & Walkley, 1956: 324 (citation of type species); Masner, 1961: 158 (junior synonym of *Gryon* Haliday).

Plastogryon Kieffer, 1908: 119, 141 (original description. Type: *Plastogryon foersteri* Kieffer, designated by Brues (1908)); Brues, 1908: 51 (diagnosis, list of species, type designation); Kieffer, 1910: 65, 81 (description, list of species,

keyed); Dodd, 1913a: 131 (keyed); Kieffer, 1913: 230, 245 (description, key to species of Europe and Algeria); Dodd, 1915: 24 (key to species of Australia); Dodd, 1915: 24 (key to species of Australia); Kieffer, 1926: 270, 446 (description, keyed, key to subgenera, key to species); Jansson, 1939: 172 (keyed); Muesebeck & Walkley, 1956: 385 (citation of type species); Masner 1961: 158 (junior synonym of *Gryon* Haliday).

Psilacolus Kieffer, 1908: 179, 180 (original description. Type species: *Acolus xanthogaster* Ashmead, designated by Kieffer (1926)); Brues, 1908: 47 (diagnosis, list of species); Kieffer, 1910: 100, 101 (description, list of species, keyed); Kieffer, 1912: 88 (description); Dodd, 1914a: 59 (keyed); Kieffer, 1926: 132, 151 (description, keyed, key to species); Muesebeck & Walkley, 1956: 393 (citation of type species); Muesebeck & Masner, 1967: 299 (junior synonym of *Gryon* Haliday).

Holacolus Kieffer, 1912: 89, 106 (original description. Type species: *Acolus opacus* Thomson, designated by Muesebeck & Walkley (1956). Key to species of Europe and Algeria); Kieffer, 1926: 133, 169 (description, keyed, key to species); Jansson, 1939: 173 (keyed); Maneval, 1940: 111 (keyed); Muesebeck & Walkley, 1956: 359 (designation of type species); Masner, 1961: 158 (junior synonym of *Gryon* Haliday).

Plesiobaeus Kieffer **syn. rev.**, 1913: 229, 282 (original description. Type: *Plesiobaeus hospes* Kieffer, by monotypy); Kieffer, 1926: 271, 556 (description, keyed); Morley, 1929: 54 (catalog of species of Britain); Jansson, 1939: 172 (keyed); Maneval, 1940: 112 (keyed); Muesebeck & Walkley, 1956: 386 (citation of type species); Szabó, 1966: 422 (keyed); Kozlov, 1971: 38 (keyed); Fergusson, 1978: 118 (checklist of species of Britain); Kozlov, 1978: 621 (description); Mineo, 1979a: 248 (junior synonym of *Gryon* Haliday); Masner, 1980: 13 (keyed); Kozlov & Kononova, 1990: 96, 265, 307 (description, keyed); Fabritius & Popovici, 2007: 11, 34, 63 (description, keyed); Kononova & Kozlov, 2008: 25, 445 (description, keyed, treated as valid genus).

Comments. Mineo (1979a) stated that *Plesiobaeus hospes* seemed to be conspecific with *Gryon misellum* based on its original description. He also stated that the type was examined but did not provide characters based on this examination to support the generic transfer. Mineo and Caleca (1987b) reported that the species in this group, containing only *G. hospes*, had a 1-2-2-0 claval formula, which is consistent with some species of *Gryon*, e.g., *G. moczari*, whereas no species of *Hadronotus* known to us has such a claval formula.

Hadronotellus Kieffer, 1917: 341 (original description. Type: *Hadronotellus pedester* Kieffer, by monotypy and original designation. Synonymized by Kieffer (1926)); Muesebeck & Walkley, 1956: 357 (citation of type species); Szabó, 1966: 421, 422 (description, key to Palearctic species known to the author, keyed); Hellén, 1971: 5, 22 (description, keyed).

Heterogryon Kieffer, 1926: 271, 446, 448 (original description. Type: *Plastogryon sagax* Kieffer, designated by Muesebeck & Walkley (1956). Proposed as a subgenus of *Plastogryon*, keyed. Synonymized by Masner (1961)); Muesebeck & Walkley, 1956: 359 (designation of type species); Masner, 1961: 158 (junior synonym of *Gryon* Haliday).

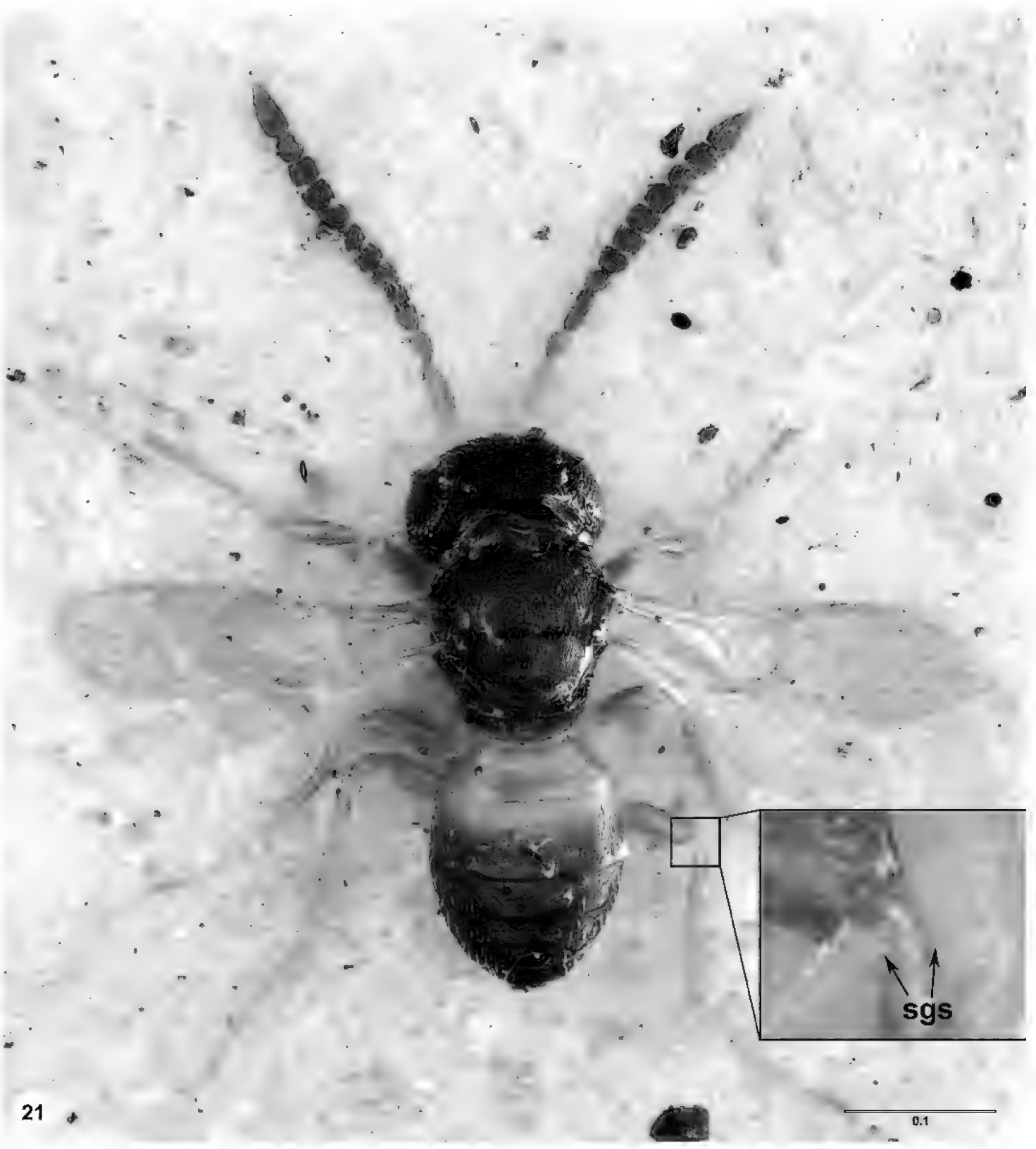
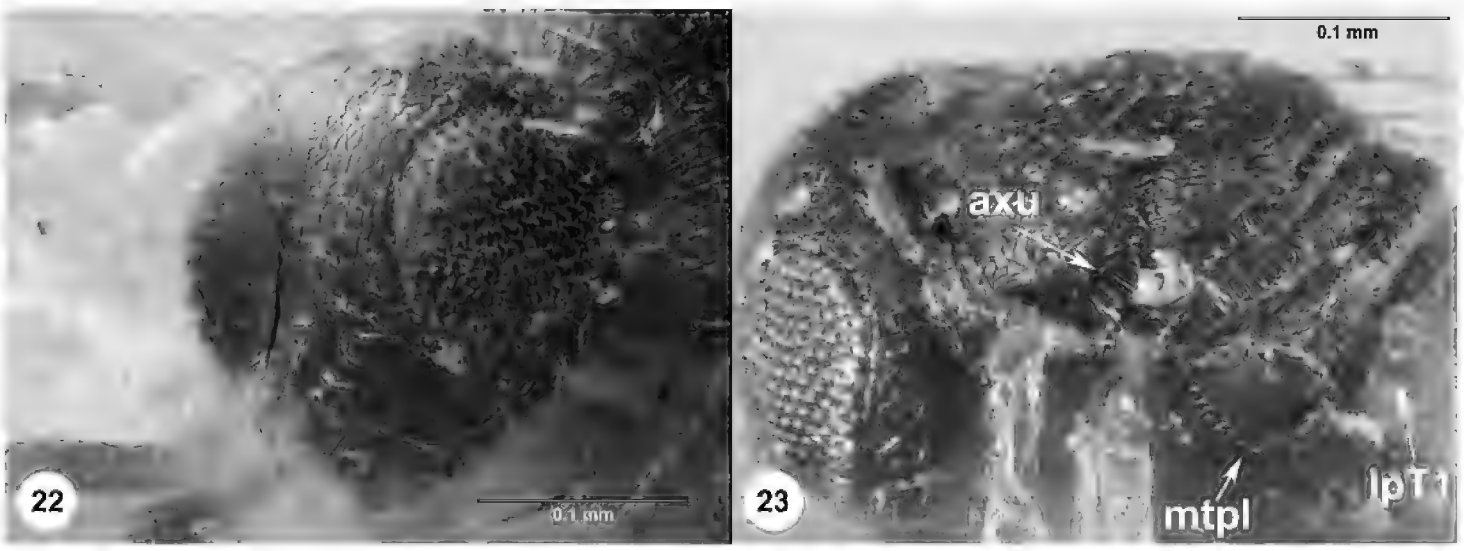


Figure 21. *Gryon misellum*, lectotype male (NMINH_2018_11_02), dorsal view.

Eremioscelio Priesner **syn. rev.**, 1951: 129 (original description. Type: *Eremioscelio cydnoides* Priesner, by monotypy and original designation); Muesebeck & Walkley, 1956: 351 (citation of type species); Kozlov, 1963a: 354, 357 (description, keyed); Kozlov, 1963b: 661, 666 (description, keyed); Kozlov, 1971: 38, 49 (synonymy, keyed); Kozlov, 1972: 656 (key to species); Masner, 1976: 59 (description); Kozlov, 1978: 621 (description, key to species of European USSR); Kozlov & Kononova, 1990: 95, 265, 310, 311 (description, key to species of USSR, keyed); Mineo, 1991: 1, 9 (junior synonym of *Gryon* Haliday, described as *cydnoide* species group); Johnson, 1992: 372 (cataloged, catalog of world species); Kononova, 1995: 62, 85



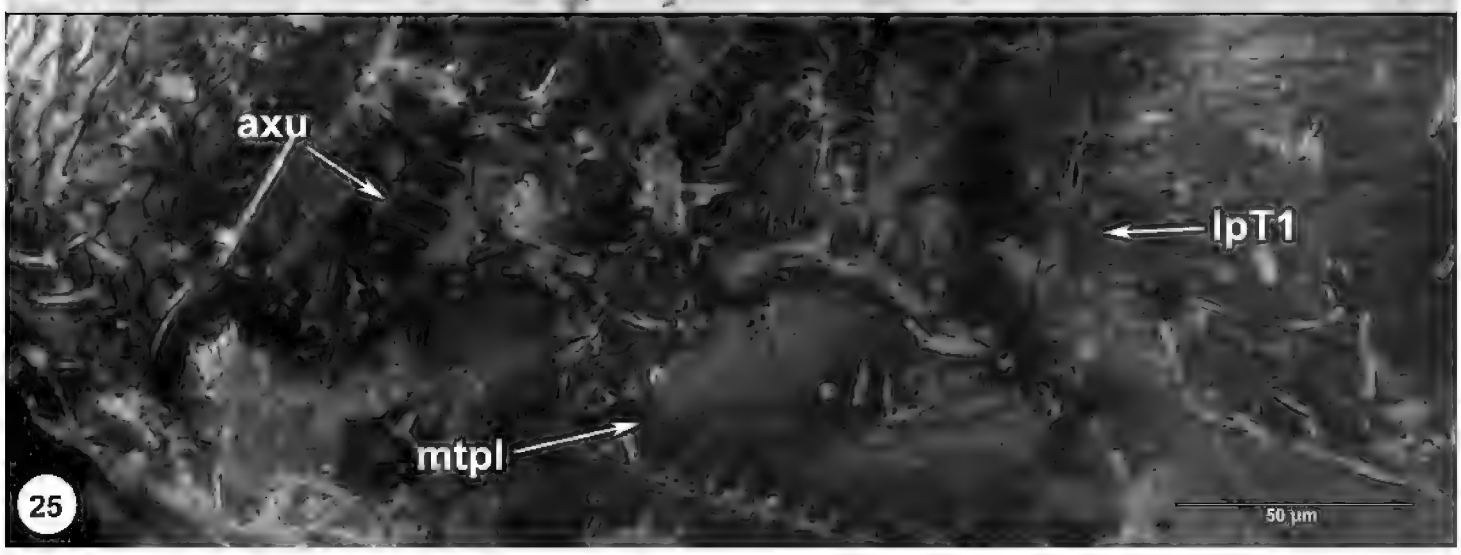
Figures 22–23. *Gryon misellum* **22** lectotype male (NMINH_2018_11_02), head, anterolateral view **23** paralectotype female (NMINH_2018_11_03), head, mesosoma, metasoma, dorsolateral view.

(keyed, diagnosis, key to species of Russian Far East); Fabritius & Popovici, 2007: 11, 36, 63 (description, key to Romanian species, keyed); Kononova & Kozlov, 2008: 25, 451 (description, keyed, key to species of Palearctic region, treated as a valid genus).

Comments. Images of the holotype specimen of *Eremioscelio cydnoides* illustrate important diagnostic characters of *Gryon*: the lateral pit on T1 and the presence of subgenual spines (Figures 31, 33). Examination of additional material revealed that the clypeus is anteriorly projecting with sharp corners (Figure 30) and that the axillula is striate (Figures 32, 34). The transverse, wavy sculpture on the mesoscutum and mesoscutellum of this species is an oddity for the genus (Figures 31–32).

Hungarogryon Szabó **syn. n.**, 1966: 422, 443 (original description. Type: *Hungarogryon moczari* Szabó, by monotypy and original designation, keyed); Kozlov, 1971: 38 (keyed); Kozlov, 1978: 621 (description); Masner, 1980: 13 (keyed); Kozlov & Kononova, 1990: 96, 265, 320 (description, keyed); Johnson, 1992: 402 (cataloged, catalog of world species); Fabritius & Popovici, 2007: 63 (keyed); Kononova & Kozlov, 2008: 25, 461 (description, keyed).

Comments. *Gryon moczari* (=*Hungarogryon moczari*) was the sole species in *Hungarogryon*, and is very small, only slightly longer than 0.5 mm in length. We place this species in *Gryon* based on the presence of subgenual spines on the hind tibia (Figure 38), a frons without transverse sculpture in the frontal depression (Figure 35), a protruding clypeus with sharp corners (Figure 35), and the lateral pit on T1 (Figure 37). However, in two characters, *Gryon moczari* differs from the rest of *Gryon*: the axillula is mostly smooth with crenulae present only along the anterodorsal margin (Figure 36) and the antenna has three clavomeres instead of the usual four (Figure 39). We consider it most likely that these characters are derived within the genus and are related to reduction in body size. The forewing has a fringe of long, delicate setae. The slide-mounted wing illustrated in Figure 40 retains only one of these setae.



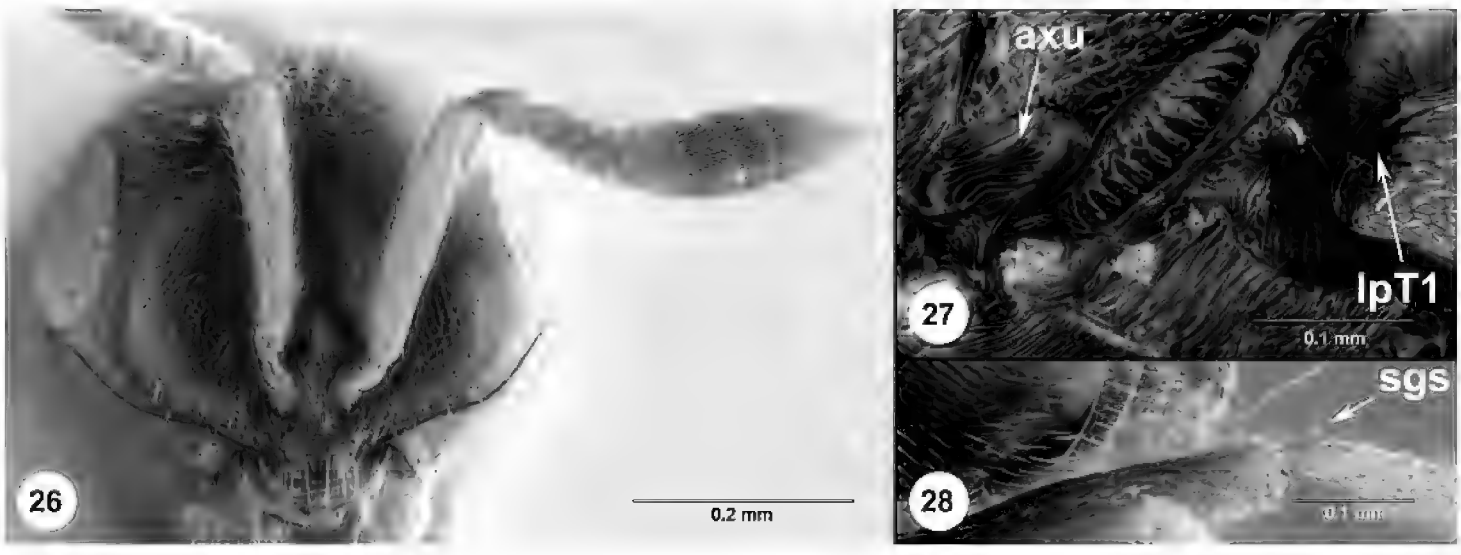
Figures 24–25. *Gryon misellum*, paralectotype female (NMINH_2018_11_03) **24** habitus, dorsolateral view **25** mesosoma and T1, dorsolateral view.

Masneria Szabó, 1966: 422, 442 (original description. Type: *Hadronotus lymantriae* Masner, by monotypy and original designation, keyed. Synonymized by Masner (1976)); Masner, 1976: 57 (junior synonym of *Gryon* Haliday).

Pannongryon Szabó, 1966: 422, 435 (original description. Type: *Pannongryon szelenyii* Szabó, by original designation. Key to species known to author, keyed. Synonymized implicitly by Kozlov (1971), explicitly by Masner (1976)); Kozlov, 1971: 47 (junior synonym of *Gryon* Haliday).

Sundholmia Szabó, 1966: 422, 438 (original description. Type: *Sundholmia nitens* Szabó, by monotypy and original designation, keyed. Synonymized by Mineo (1980a)); Kozlov, 1971: 38 (keyed); Mineo, 1980a: 200 (junior synonym of *Gryon* Haliday).

Breviscelio Sundholm **syn. n.**, 1970: 383 (original description. Type: *Breviscelio crenatus* Sundholm, by monotypy and original designation); Mineo & Villa, 1982b: 175 (taxonomic value of pleural structures, clypeus, and antennal sensilla); Mineo

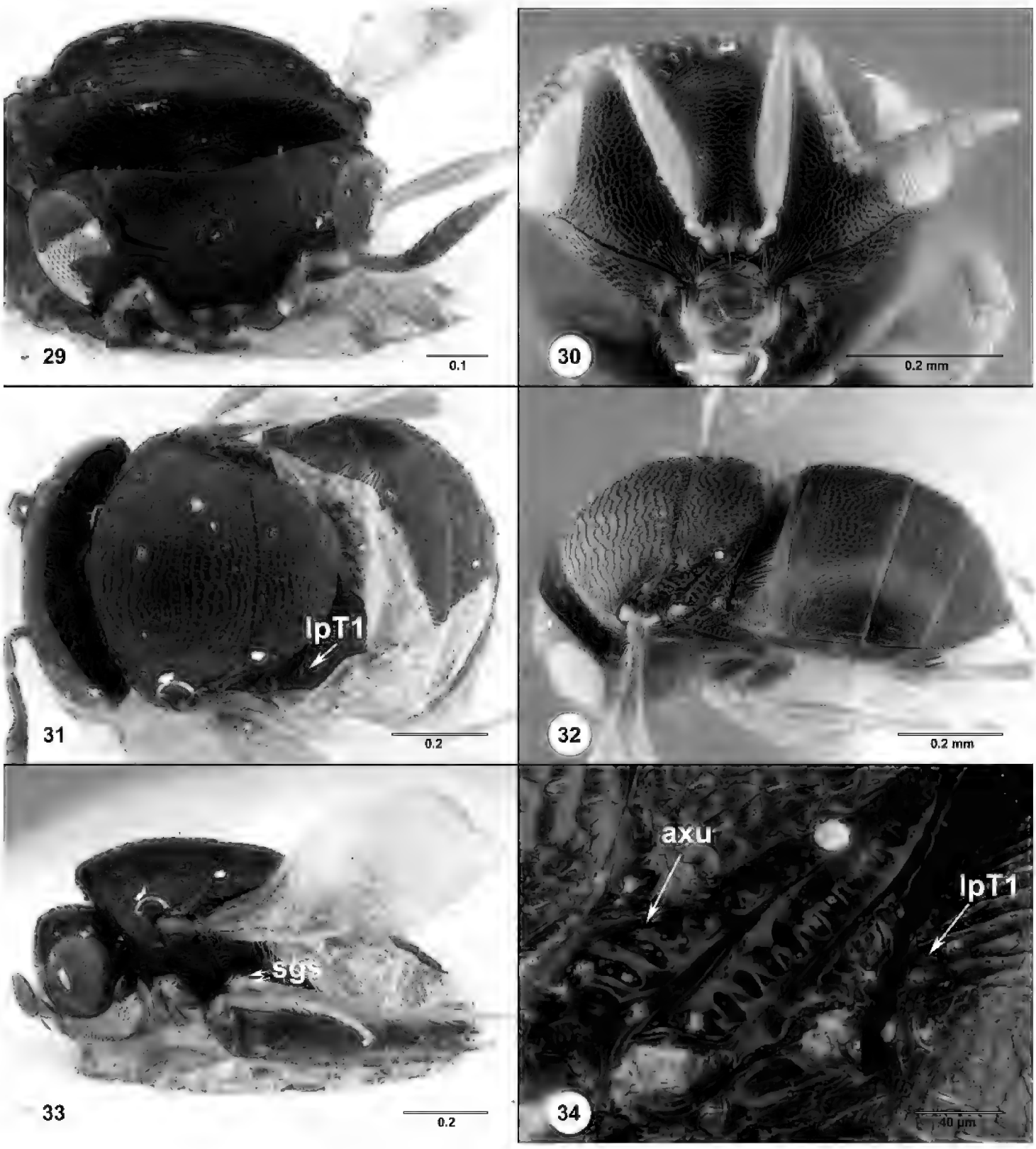


Figures 26–28. *Gryon paradigma* (CNC664037) **26** head, anterior view **27** mesosoma and T1, dorsolateral view **28** hind leg, lateral view.

& Villa, 1982a: 138 (taxonomic value of structures on the posterior surface of the head); Caleca, 1990b: 139 (description); Johnson, 1992: 354 (cataloged, catalog of world species); Caleca, 1992: 52, 53 (key to species, discussion of relationships); Austin & Field, 1997: 39, 68 (structure of ovipositor system, discussion of phylogenetic relationships).

Comments. Our treatment of *Breviscelio* as a junior synonym of *Gryon* is supported by molecular and morphological evidence. Specimens of *Gryon crenatum* (=*Breviscelio crenatus*, the type species of *Breviscelio*) were retrieved within the *Gryon* clade in the 4-gene and COI analyses. The striate axillula and the lateral pit on T1 are visible in the holotype specimen (Figure 41). Figures 42–46 illustrate other specimens of *Gryon crenatum* from South Africa, showing that this species also has the suite of characters used to diagnose *Gryon*: antennal scrobe without transverse sculpture (Figure 42); head and dorsal mesosoma covered with microsculpture (Figures 42–44); metapleuron mostly glabrous and undivided by change in sculpture or setation (Figure 43), subgenual spines present on the hind tibia (Figure 46). The conspicuous frontal ridge in *G. crenatum* is associated with an elongation and oblique orientation of the mandibles. This association is known from other platygastroids, including *Encyrtoscelio* Dodd, *Tyrannoscelio* Masner, Johnson & Arias-Penna, *Acanthoscelio* (Scelionidae) and *Sparasion* Latreille (Sparasionidae) (Figures 47–50) and may be an adaptation for using the mandibles to dig through soil. *Gryon crenatum* has spines throughout the tibiae and tarsi on all legs and unusual spatulate setae found on the fore tarsus (Figure 45), which may also be adaptations for fossorial behavior.

Exon Masner **syn. rev.**, 1980: 12, 22 (original description. Type: *Exon californicum* Masner, by original designation, keyed. Synonymized by Mineo (1980b)); Mineo, 1980b: 215 (junior synonym of *Gryon* Haliday); Kozlov & Kononova, 1990: 95, 265, 308 (description, key to species of USSR, keyed); Kononova & Petrov, 2002: 57 (description, key to species of Palearctic); Fabritius & Popovici, 2007: 11, 41, 63 (description, keyed); Kononova & Kozlov, 2008: 25, 446 (treated as valid genus, description, keyed, key to species of Palearctic region).



Figures 29–34. *Gryon cydnoide* **29** holotype female (USNMENT01059665), head and mesosoma, anterior view **30** female (OSUC 395743) head, anterior view **31** holotype female (USNMENT01059665), habitus, dorsal view **32** female (OSUC 395739), habitus, dorsolateral view **33** holotype female, habitus, lateral view **34** mesosoma and T1, dorsolateral view.

Comments. Like *Eremioscelio*, *Exon* has moved in and out of *Gryon* since it was first described. Our examination of a paratype specimen indicates that it belongs in *Gryon*. The antennal scrobe lacks transverse sculpture, the metapleuron is mostly glabrous and undivided, and striation of the axillula is visible (Figures 51–52). Figure 53 illustrates the dorsal metasoma. The quality of the image does not enable us to see the lateral pit on T1, but the uniform size of the foveae along the anterior margin of T1 is apparent, and this supports its placement in *Gryon*.

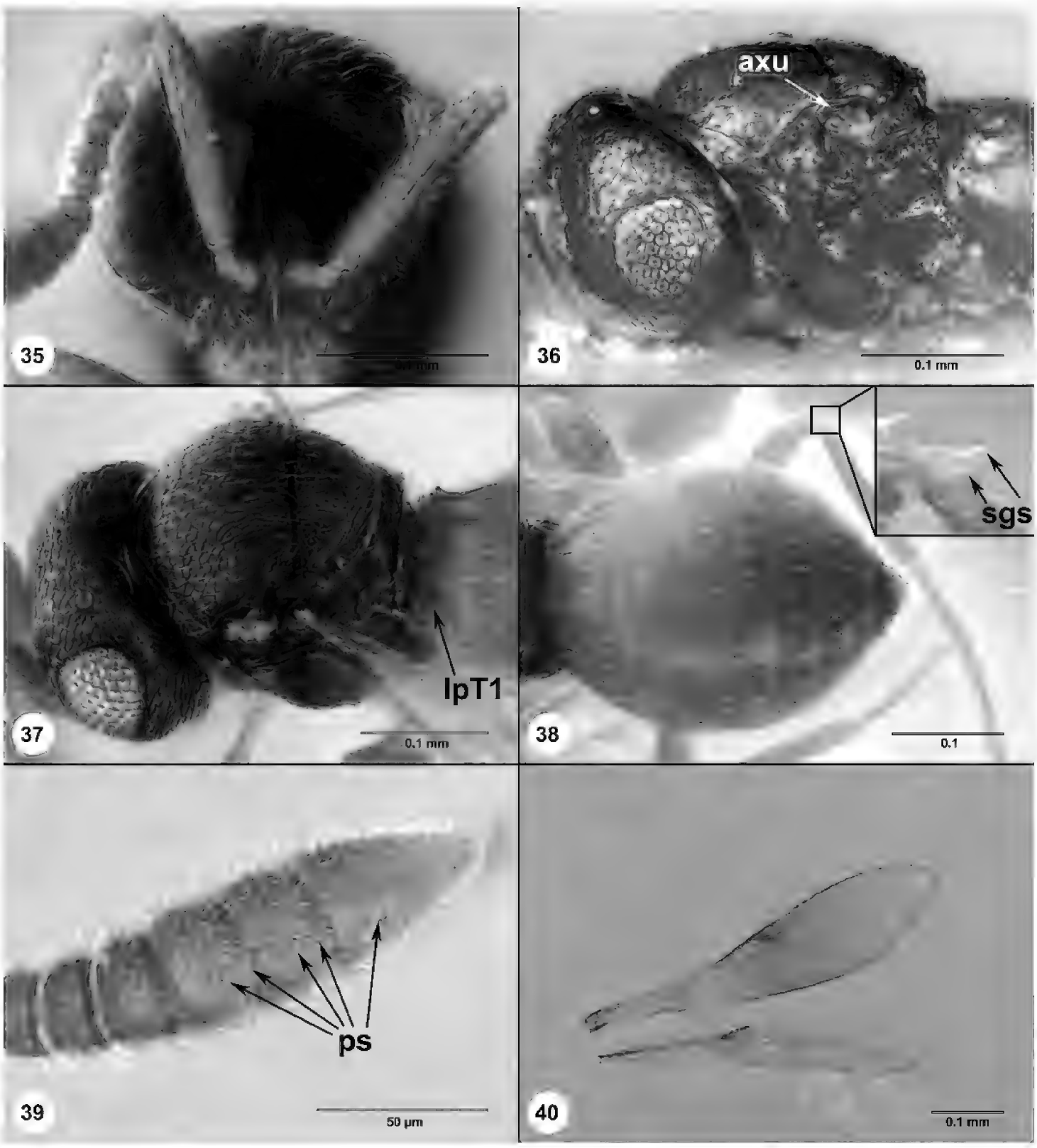
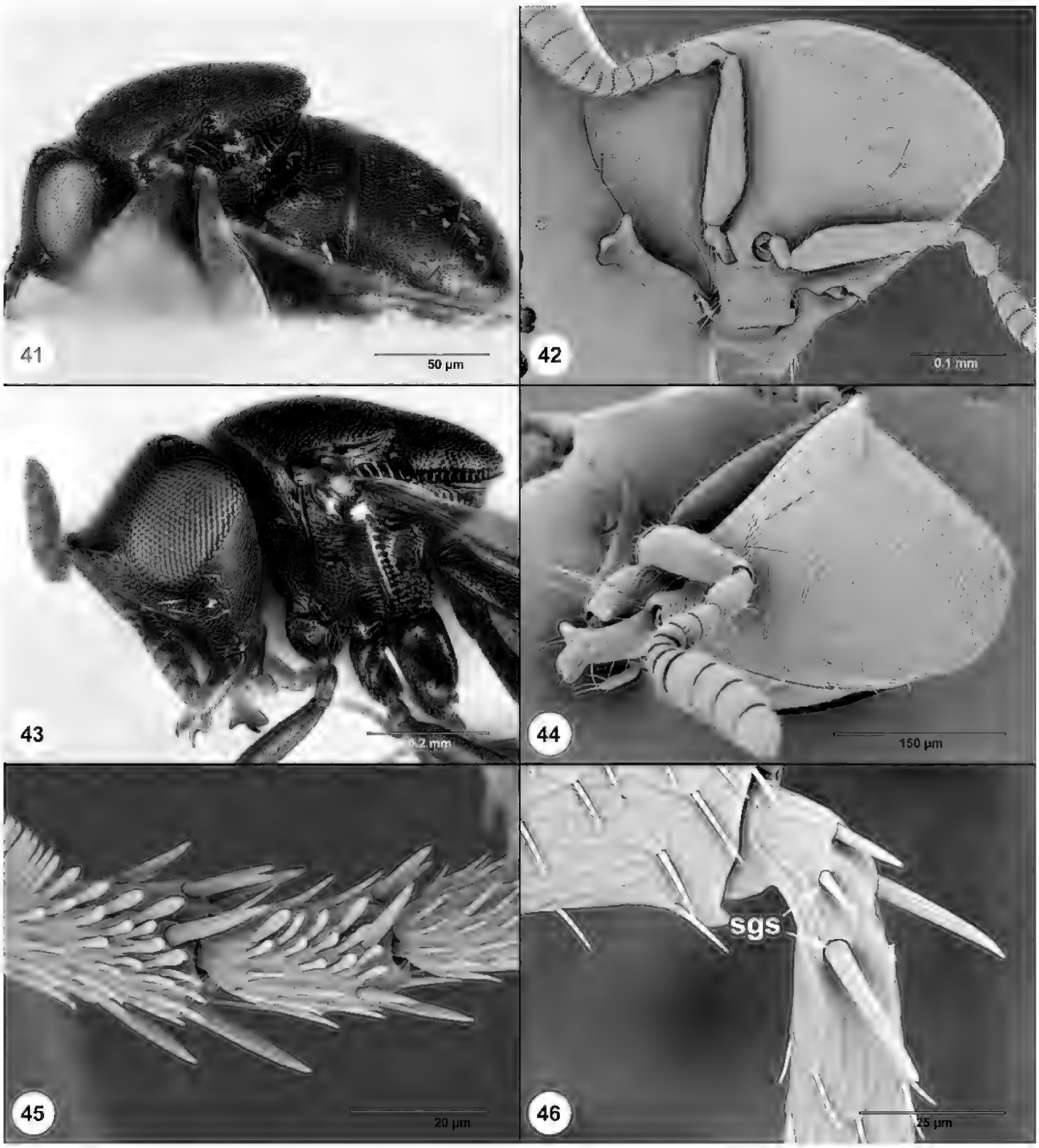


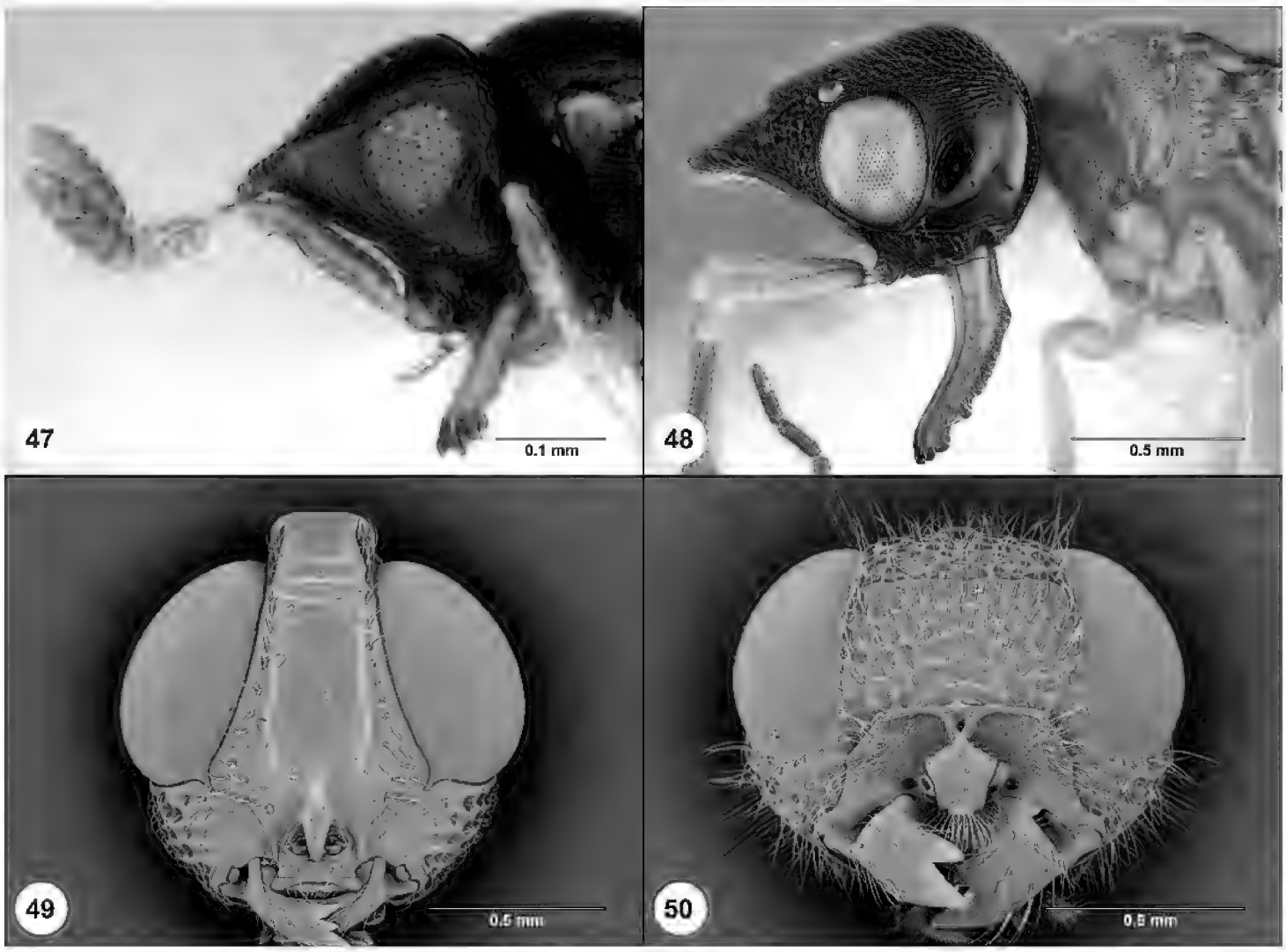
Figure 35–40. *Gryon moczari* **35** female (CNC664036), head, anterior view **36** holotype female, head and mesosoma, lateral view **37** female (CNC664036), head and mesosoma, dorsolateral view **38** female (CNC664036), metasoma, dorsal view **39** female (CNC664036), antennal clava, ventrolateral view **40** female (CNC664036), wings, dorsal view.

Diagnosis. Head with coriaceous microsculpture throughout; mandibles usually bidentate with teeth large and roughly equal in size, sometimes tridentate with medial tooth the smallest; clypeus projecting, typically with pointed corners; ventral frons sometimes with weakly indicated facial striae; central keel present or absent; antennal scrobe convex to concave, without transverse rugae or striation, never delimited by carinae; female antenna with ten flagellomeres (nine in *G. paradigma*) and four clavomeres (three in *G. moczari*); mesoscutum and mesoscutellum with coriaceous microsculpture throughout, occasion-



Figures 41–46. *Gryon crenatum* **41** holotype female (MZLU Type no. 911:1), habitus, dorsolateral view **42** female (SAM-HYM-P093658), head, anterior view **43** female (SAM-HYM-P093675), head and mesosoma, lateral view **44** female (SAM-HYM-P093658), head, lateral view **45** female (SAM-HYM-P093658), fore tarsus, lateral view **46** female (SAM-HYM-P093658), subgenual spines on hind tibia, posterolateral view.

ally with longitudinal striation or microsculpture in the form of transverse waves; epomial carina absent or weakly developed; netrion absent; mesoscutal suprahumeral sulcus absent; mesoscutal humeral sulcus absent or indicated by a smooth furrow; mesoscutum without humeral pit (sensu Chen et al., 2020); axillula obliquely striate; metapleuron with 1–3 setae in anterodorsal corner, sometimes with a single seta in dorsal metapleural area, otherwise glabrous; metapleuron undivided dorsoventrally by a change in sculpture



Figures 47–50. 47 *Encyrtoscelio* (OSUC 334153), head, lateral view **48** *Tyrannoscelio genieri* Masner & Johnson (OSUC 545772), head and mesosoma, lateral view **49** *Acanthoscelio* (OSUC 232241), head, anterior view **50** *Sparasion philippinensis* (USNMENT00872835), head, anterior view.

or setation; hind tibia with one or two pairs of subgenual spines; foveae along anterior T1 roughly equal in size, ending in a sublateral carina followed by a lateral pit.

The two most unusual species, as far as diagnostic characters are concerned, are *G. moczari* and *G. paradigma*. The former is discussed in the comments section for the synonymy of *Hungarogryon*. *Gryon paradigma* is unusual in that the females have eleven antennomeres instead of twelve, the ventrolateral corners of the clypeus are not pointed, and the axillular striae are wavy and irregular (Figures 26–28). This species otherwise complies with the diagnosis above and we consider it to be a derived species of *Gryon*.

Species of *Gryon*

***Gryon aetherium* Talamas, sp. nov.**
http://zoobank.org/75100840-5BF1-4FEC-9B53-880F0E221074
Figures 5, 9, 15–16, 54–72.

Description. Color of body: dark brown to black. Color of legs: coxae and femora brown; trochanters, tibiae and tarsi yellow to pale brown.

Figures 51–53. *Gryon californicum*, paratype female (USNMENT01109308) **51** habitus, lateral view **52** head, anterior view **53** metasoma, dorsal view.

Color of antenna in female: yellow to pale brown, A9–A12 generally darker than preceding antennomeres.

Head: Number of mandibular teeth: 2. Shape of mandibular teeth: large, teeth roughly equal in size. Shape of clypeus: projecting ventrally, apex flat to convex, with sharp lateral corners. Number of clypeal setae: 6. Epiclypeal carina: absent. Facial striae: present as lines of microsculpture. Central keel: present. Line of setae above interantennal process: absent. Malar striae: present as lines of microsculpture. Genal carina: absent. Hyperoccipital carina: absent. Anterior margin of occipital carina on gena: smooth. Occipital carina: present dorsally and in ventral portion of gena, absent or weakened posterodorsal to compound eye.

Mesosoma: Epomial carina: absent. Sculpture of lateral pronotum: reticulate microsculpture. Netrion sulcus: absent. Mesoscutal suprahumeral sulcus: absent. Mesoscutal humeral sulcus: absent. Sculpture of mesoscutum: reticulate microsculpture.

Sculpture of mesoscutellar disc: reticulate microsculpture. Posterior mesoscutellar sulcus: foveate. Posterior margin of mesoscutellum: extending over metanotum, metascutellum not visible in dorsal view. Posterior margin of metascutellum: slightly convex. Sculpture on posteroventral surface metascutellum: weakly rugulose. Sculpture of metanotal trough: foveate. Length of postmarginal vein in fore wing: about 1.5 times as long as stigmal vein. Length of marginal vein in fore wing: about half as long as stigmal vein.

Wing color: hyaline with transverse band of infuscation posterior to marginal vein. Shape of submarginal vein: straight in basal 4/5, with dip proximal to reaching wing margin.

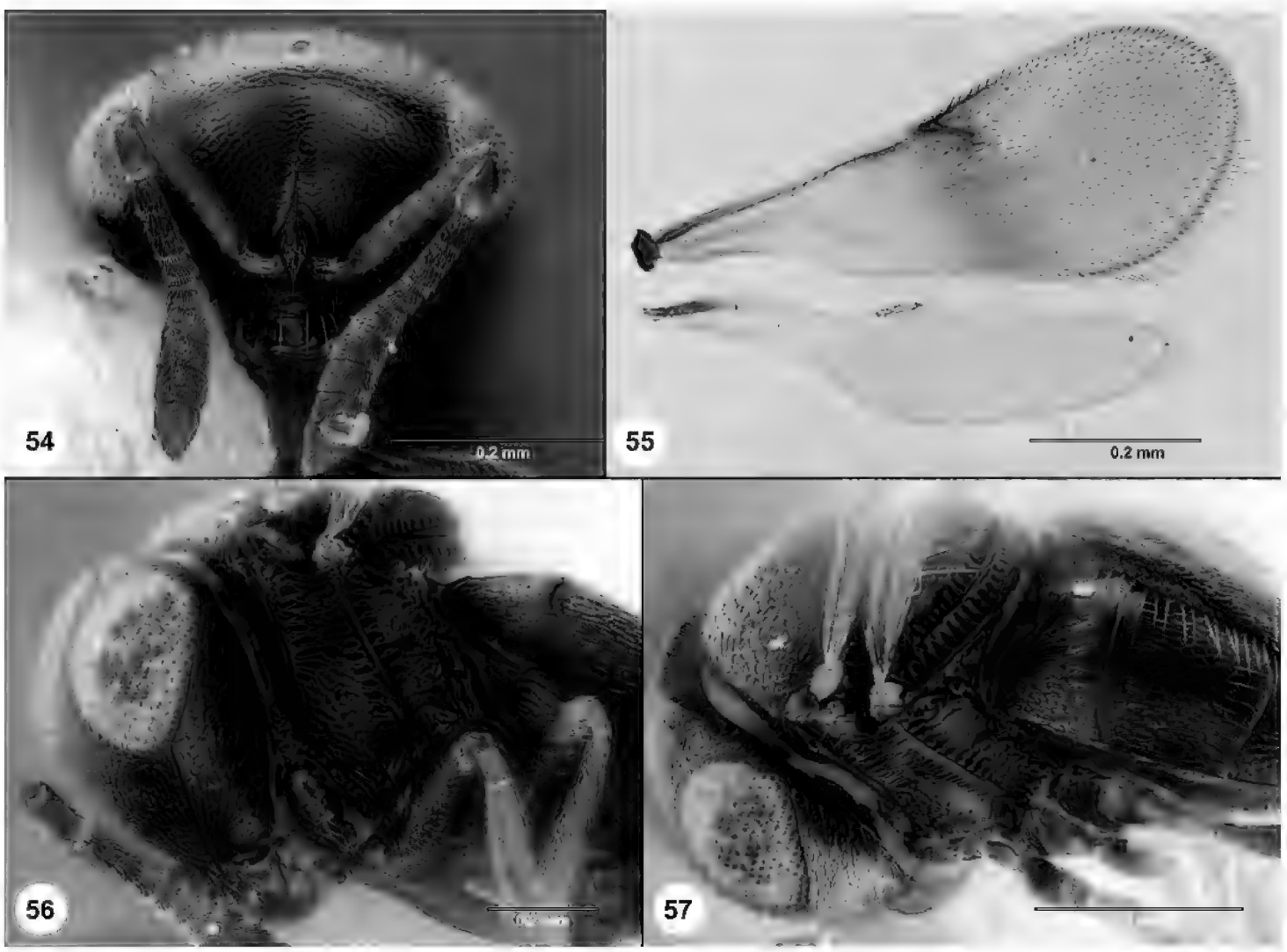
Lateral propodeal carina: continuous across posterior propodeum, forming flange around metasomal depression. Sculpture of metasomal depression: weakly rugulose. Sulcus of the propodeal foramen: foveate dorsally, absent ventrally. Cells or foveae along ventral margin of mesopleural carina: absent. Posterior limit of acetabulum: acetabular carina intersecting with ventral mesopleural carina. Postacetabular sulcus: foveate. Mesopleural epicoxal sulcus: foveate. Episternal foveae: present. Mesopleural carina: absent; present only at ventral apex of femoral depression. Sculpture of anteroventral mesopleuron: reticulate microsculpture. Sculpture of femoral depression: smooth. Prespecular sulcus: foveate. Sculpture of speculum: finely striate. Shape of subalar pit: circular. Mesepimeral sulcus: comprised of transverse foveae, foveae absent or reduced in size posterior to speculum. Sculpture of posterior mesepimeral area: smooth. Paracoxal sulcus: indicated by transverse foveae, extending below metapleural pit but not to ventral margin of metapleuron. Metapleural epicoxal sulcus: indicated by crenulae or indistinguishable from rugose sculpture. Metapleural structure: not divided into anterior and posterior areas. Sculpture of dorsal metapleural area: transversely striate. Sculpture of ventral metapleural area: irregularly rugose.

Metasoma: Macrosculpture of T1: longitudinally striate, smooth along posterior margin. Setation of T1: present lateral and posterior to lateral pit of T1. Setation of T2–T5: dense in lateral part of tergite, absent medially except for a transverse line of sparse setae along posterior margin. Posterior margin of T6: concave. Sculpture of T2–T4: finely reticulate with a smooth band along posterior margin. Sculpture of S2: finely reticulate. Setation of laterotergites: present. Transverse sulcus on anterior S2: present as a line of small foveae.

Etymology. The species epithet "aetherium" derives from Latin, meaning of the sky or heavens, and refers to the unexpected appearance of this species in North America, far from its native range.

Diagnosis. *Gryon aetherium* is best separated from other *Gryon* species by the following characters: mesopleural carina entirely absent or present only at ventral apex of mesopleuron; posterior margin of mesoscutellum protruding posteriorly, concealing metascutellum and metanotal trough in dorsal view; mesopleuron with two episternal foveae; foveae of mesepimeral sulcus attenuating in size dorsally, foveae small or undefined posterior to speculum; acetabular carina and ventral mesopleural carina intersecting ventrally; metapleuron not transversely striate throughout; fore wing with infuscation posterior to marginal vein; hind tibia with four subgenual spines; lateral propodeal carina horizontal, extending laterally to metapleural carina.

In North America, *Gryon aetherium* is most similar to *G. myrmecophilum*, from which it is most easily separated by the mesopleural carina: complete in *G. myrmecophilum*, extending from the posteroventral apex of the femoral depression to the anterior margin of the mesopleuron; absent or present only at ventral apex of mesopleuron in *G. aetherium*. This character also serves well to separate *G. aetherium* from *G. gonikopalense* (Figures 77–78) *G. fasciatum* (73–76), and *G. oligomerum* Kononova, which are Old World species that are very similar to *G. aetherium* but have a complete mesopleural carina.



Figures 54–57. *Gryon aetherium* **54** holotype female (USNMENT01335778), head, anterior view **55** female (FSCA 00090468), wings, dorsal view **56** holotype female (USNMENT01335778), head, mesosoma, metasoma, lateral view **57** holotype female (USNMENT01335778), head, mesosoma, metasoma, dorsolateral view.

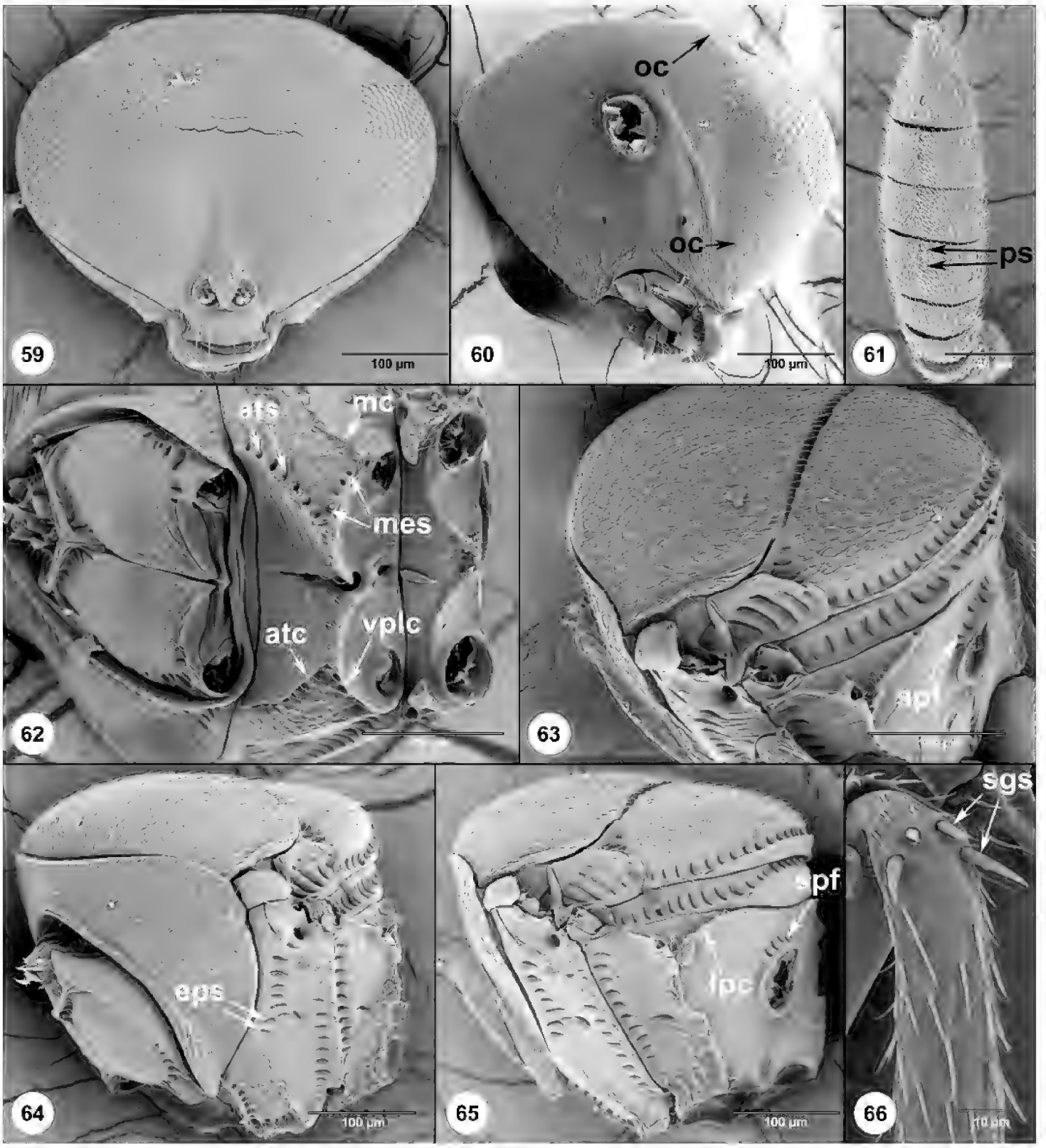
Intraspecific variation. Non-target testing of *G. aetherium* in quarantine enabled us to examine how different hosts affect the phenotype of the parasitoids. Overall, we found very little variation between specimens of *G. aetherium* reared from *Bagrada hilaris*, *Thyanta custator*, *Holcostethus*, *Banasa sordida* and *Euschistus conspersus* (Figures 67, 69–72). The sculpture of the dorsal metapleural area varies from transversely striate to irregularly rugose. The foveae that comprise the mesepimeral sulcus decrease in size dorsally, and posterior to the speculum these foveae can be small and circular or poorly defined. Only one male specimen emerged from eggs of *Banasa sordida* (Figure 71), which was unusual in that the femoral depression was faintly microsculptured and the foveae of the paracoxal sulcus were shallow and not well-defined. This specimen also had malformed antennae, suggesting that *Banasa sordida* is not a suitable host for *G. aetherium*.

Prior misidentifications. *Gryon aetherium* was misidentified twice by the first author: as *G. gonikopalense* in Martel et al. (2019) and this name was subsequently used in Martel and Sforza (2021), Tofangsazi et al. (2020) and Hougardy and Hogg (2021), and as *G. myrmecophilum* in Felipe-Victoriano et al. (2019). The morphological limits of *G. aetherium* were unclear at the time that these names were used, resulting in a hesitancy to describe it as a new species, especially because not all relevant types had been examined.

Figures 58. *Gryon aetherium*, female (USNMENT01109155), habitus, ventrolateral view.

Adventive populations. As implied by the previous paragraph, *G. aetherium* has been present in Mexico since at least June of 2018 and the study by Felipe-Victoriano et al. (2019) is thus the first record of this species in North America. It appears that *G. aetherium* has been in the United States for a similar length of time given that specimens were recovered from two locations in California: Davis, Yolo County, in 2020, and Monterey County, in 2018 and 2019. In both cases the specimens were reared from *B. hilaris* sentinel egg masses. A specimen from the 2018 collection (FSCA 00033319:PL11) was sequenced to confirm its identity (Figure 4). It differed from the quarantine populations by three base pairs, alleviating concerns that it represented escapees. The specimens collected in Monterey were stored in isopropanol, which affected the color of the specimens (Figure 68) and degraded the DNA. We were not able to amplify COI from the specimens collected in Monterey, but our morphological analysis using scanning electron microscopy finds them to be identical to the specimens in quarantine and those that were retrieved in Yolo County. In 2021, a population of *G. aetherium* was recovered in Chile, reared from the eggs of *B. hilaris* (Rojas-Gálvez et al. 2021).

Material examined. *Holotype*, female: **Pakistan:** Punjab, Toba Tek Singh, Dabanwala leg. R. Mahmood, coll. 5–9.IV.2016, ex. eggs *Bagrada hilaris* 11-V-2016 on mustard, introduced to quarantine for EBCL colony, PP8, USNMENT01335778 (deposited in USNM). *Paratypes* (72 females, 37 males): **Mexico:** 9 females, 3 males, FSCA 000900442–00090443, 000900446–00090447, 000900468–00090475 (FSCA). **Pakistan:** 19 females, 8 males, FSCA 00033215–00091216, 00091221, 00094940–00094944, 00094984–00094992; USNMENT00989933, 01109043, 01109046–01109047, 01109049, 01109052, 01109054–01109155, 01335774, 01335776 (USNM). **United States:** 44 females, 26 males, FSCA 00033319, 00090933, 00091210, 00091217,00091930, 00094869, 00094871, 00094873–00094874, 00094877, 00094885, 00094899, 00094901–00094903, 00094945– 00094981, 00094983, 00094993–00095009 (FSCA).



Figures 59–66. *Gryon aetherium* **59** female (FSCA 00094873), head, anterior view **60** female (FSCA 00094869), head, posterolateral view **61** female (FSCA 00094873), antennal clava, lateral view **62** female (FSCA 00094869), mesosoma, ventral view **63** female (FSCA 00094873), mesosoma, dorsolateral view **64** female (FSCA 00094874), mesosoma, anterolateral view **65** female (FSCA 00094874), mesosoma, posterolateral view **66** female (FSCA 00094871), hind tibia, dorsal view.

Gryon africanum Mineo

Holotype images: https://zenodo.org/record/4498963#.YBsDc3lOlaQ

Gryon africanum Mineo, 1991: 19 (original description, assigned to *myrmecophilum* species group).

Figures 67–72. *Gryon aetherium*, lateral habitus **67** female (FSCA 00094902), ex. *Bagrada hilaris* **68** female (FSCA 00094885), ex. *Bagrada hilaris* **69** female (FSCA 00094903), ex. *Holcostethus* **70** female (FSCA 00094899), ex. *Thyanta custator* **71** male (FSCA 00094877), ex. *Banasa sordida* **72** male (FSCA 00094901), ex. *Euschistus conspersus*.

Gryon amphiboli Mineo

Paratype images: https://zenodo.org/record/4924883#.YMJ6RHpKhaQ

Gryon amphiboli Mineo, 1991: 19 (original description, assigned to *myrmecophilum* species group).

Comments. This species remains in *Gryon* based on its assignment to the *myrmecophilum* species group.

Gryon amplum (Dodd)

Hadronotus amplus Dodd, 1914b: 81 (original description); Dodd, 1915: 20 (keyed); Kieffer, 1926: 455, 471 (description, keyed).
Mirotelenomus amplus (Dodd): Dodd, 1926: 313 (generic transfer); Galloway, 1976: 96 (type information); Johnson, 1992: 439 (cataloged, type information).
Gryon amplum (Dodd): Caleca & Mineo, 1995: 19 (generic transfer).

Comments. The original description states "Head and thorax very finely reticulate rugulose" which is consistent with placement in *Gryon* if it is referring to microsculpture. However, it also states "club 6-jointed", which suggests *Hadronotus*. Because it is presently unclear where this species belongs, we leave it in its current placement.

Gryon angustipenne (Dodd)

Holotype images: https://zenodo.org/record/4721639#.YIcPhPlKhaQ

Telenomoides angustipennis Dodd, 1913a: 169, 171 (original description, keyed).
Hadronotus angustipennis (Dodd): Dodd, 1914a: 129 (generic transfer); Dodd, 1915: 20 (keyed); Kieffer, 1926: 456, 471 (description, keyed).
Mirotelenomus angustipennis (Dodd): Dodd, 1926: 313 (generic transfer); Galloway, 1976: 96 (type information); Johnson, 1992: 439 (cataloged, type information).
Gryon angustipenne (Dodd): Caleca & Mineo, 1995: 19 (generic transfer).

Comments. The holotype specimen has a 4-merous clava, the carina adjacent to the lateral pit on T1 is clearly visible, and the striation inside the axillar crescent is visible in the image of the right side. These characters, combined with the lack of macrosculpture on the head and dorsal mesosoma, enable us to confidently place this species in *Gryon*.

Gryon anna Kozlov & Kononova

Gryon anna Kozlov & Kononova, 1989: 80, 96 (original description, keyed); Kozlov & Kononova, 1990: 268, 298 (description); Johnson, 1992: 379 (cataloged, type information); Kononova, 1995: 85 (keyed); Kononova & Petrov, 2002: 56 (keyed); Kononova & Kozlov, 2008: 332, 428 (description, keyed); Timokhov, 2019b: 47 (catalog of species of Russia).

Comments. Two characters from the original description suggest that this species belongs in *Gryon*: "Frontal depression not shallow, streaked with very fine arcuate wrinkles. The head is fine-grained." and Figure 1–5 illustrates a 4-merous clava.

Gryon arabicum (Caleca), comb. nov.

Breviscelio arabicus Caleca, 1990b: 140 (original description); Caleca, 1992: 52, 53 (type information, keyed).

Gryon ariantum Kozlov & Kononova

Gryon ariantum Kozlov & Kononova, 2004: 196 (original description); Kononova & Kozlov, 2008: 329, 402 (description, keyed).

Comments. We leave this species in *Gryon* until the type specimen can be examined directly. Figure 3–6 in Kozlov and Kononova (2004) illustrates a 4-merous clava, but the original description is otherwise not informative.

Gryon artum (Kozlov) comb. rev.

Mirotelenomus artus Kozlov, 1963a: 356 (english translation of original description, keyed); Kozlov, 1963b: 664 (original description, keyed); Szabó, 1966: 440 (description); Kozlov, 1978: 621 (description).

Exon artus (Kozlov): Masner, 1980: 22 (generic transfer); Kozlov & Kononova, 1990: 309 (description, keyed); Kononova & Petrov, 2002: 57 (keyed); Fabritius & Popovici, 2007: 41 (description).

Gryon artus (Kozlov): Mineo, 1980a: 200 (generic transfer).

Gryon artum (Kozlov): Mineo & Caleca, 1987b: 49 (emendation, keyed); Johnson, 1992: 379 (cataloged, type information); Mineo & Caleca, 1994: 122 (distribution).

Exonartum (Kozlov): Kononova & Kozlov, 2008: 447, 449 (description, keyed, generic transfer); Timokhov, 2019a: 15 (distribution); Timokhov, 2019b: 47 (catalog of species of Russia).

Comments. Kozlov (1963a) presented some characters that indicate that this species belongs in *Gryon*: mandibles bidentate, "Head, surface of thorax... with delicate alveolate sculpturing". Figures 9–9 and 9–15 in this description illustrate reduced wing venation that is noteworthy.

Gryon austrafricanum Mineo

Gryon austrafricanum Mineo, 1979a: 236 (original description); Mineo & Caleca, 1987b: 47 (description of male); Mineo, 1990: 47 (distribution); Johnson, 1992: 379 (cataloged, type information).

Comments. The original description is largely inadequate for generic placement, but it states that the mandibles are bidentate, which is consistent with this as a species of *Gryon*.

***Gryon brevipenne* (Harrington)**
Figures 113–116; Holotype images in MBD: CNC No. 2523

Hadronotus brevipennis Harrington, 1900: 188 (original description); Brues, 1910: 47 (keyed); Kieffer, 1926: 454, 465 (description, keyed).
Gryon brevipennis (Harrington): Muesebeck & Masner, 1967: 299 (generic transfer); Sarazin, 1986: 973 (type information).
Gryon brevipenne (Harrington): Masner, 1983: 135, 166 (description, emendation, lectotype designation, keyed); Johnson, 1992: 380 (cataloged, type information).

***Gryon brevium* Kononova**
Holotype images: https://zenodo.org/record/5159819#.YQq0m0RKhaQ

Gryon brevior Kononova, 2005: 1358 (original description); Kononova, Pavlicek & Nevo, 2005: 816 (description).
Gryon brevius Kononova: Kononova & Kozlov, 2008: 328, 394 (description, keyed).

Comments. This species remains in *Gryon* based on images of the holotype specimen that illustrate the striate axillula, glabrous metapleuron, and subgenual spines on the hind tibia.

***Gryon californicum* (Masner), comb. rev.**
Figures 51–53; Paratype images in MBD: USNMENT01109308

Exon californicum Masner, 1980: 22 (original description).
Gryon californicum (Masner): Mineo & Caleca, 1987b: 49, 50 (generic transfer, keyed); Johnson, 1992: 380 (cataloged, type information).

***Gryon callidum* Kozlov & Kononova**
Holotype images: https://zenodo.org/record/5599890#.YXgJM_nMJaQ
Paratype images: https://zenodo.org/record/5599902#.YXgKb_nMJaQ

Gryon callidum Kozlov & Kononova, 2004: 197 (original description); Kononova & Kozlov, 2008: 332, 430 (description, keyed); Timokhov, 2019b: 47 (catalog of species of Russia).

Gryon caudatum Kozlov & Kononova

Gryon caudatum Kozlov & Kononova, 2004: 197 (original description); Kononova & Kozlov, 2008: 326, 373 (description, keyed).

Comments. This species remains in *Gryon* based on the abstract of Kozlov and Kononova (2004) which states that it is close to *G. simile*, Figure 2–7 in that publication, which illustrates a frontal depression without transverse sculpture, and Figure 3–7, which illustrates a 4-merous clava.

Gryon chrysolaum (Walker)

Telenomus chrysolaus Walker, 1839: 80 (original description).
Hadronotus chrysolaus (Walker): Dodd, 1920a: 352 (generic transfer).
Liophanurus chrysolaus (Walker): Kieffer, 1926: 66, 84 (description, generic transfer, keyed).
Gryon chrysolaus (Walker): Masner, 1965: 75 (type information, generic transfer).
Gryon chrysolaum (Walker): Johnson, 1992: 381 (cataloged, type information).

Comments. The genus cannot be determined from the original description and examination of the primary type is required.

Gryon conicum Kozlov & Kononova

Gryon conicus Kozlov & Kononova, 1989: 79, 89 (original description, keyed); Kozlov & Kononova, 1990: 267, 282 (description, keyed); Kononova & Petrov, 2002: 55 (keyed).
Gryon conicum Kozlov & Kononova: Johnson, 1992: 381 (cataloged, type information); Kononova & Kozlov, 2008: 327, 381 (description, keyed); Timokhov, 2019b: 47 (catalog of species of Russia).

Comments. This species remains in *Gryon*, largely because we cannot reliably determine its genus without examination of the type specimen. Our translation of the original description is as follows. "Frontal impression superficial, with very thin arcuate wrinkles. The head is fine-grained." This is congruent with *Gryon* if the arcuate wrinkles refer to lines of microsculpture.

Gryon consocium Mineo

Holotype images: https://zenodo.org/record/4499111#.YBsiUHlOlaQ

Gryon consocium Mineo, 1991: 20 (original description, assigned to *myrmecophilum* species group); Mineo & Caleca, 1994: 119 (distribution).

***Gryon coracinum* (Fouts)**

Holotype images in MBD: USNMENT00989057

Synteleia coracina Fouts, 1927: 178 (original description).
Gryon coracinus (Fouts): Muesebeck & Masner, 1967: 299 (generic transfer); Masner & Muesebeck, 1968: 34 (type information).
Gryon coracinum (Fouts): Masner, 1983: 135, 172 (description, emendation, keyed); Johnson, 1992: 381 (cataloged, type information).

***Gryon cornutum* Kononova & Petrov**

Gryon cornutus Kononova & Petrov, 2001: 1471 (original description); Kononova & Petrov, 2002: 53 (keyed).
Gryon cornutum Kononova & Petrov: Kononova & Kozlov, 2008: 323, 349 (description, keyed).

Comments. This species remains in *Gryon*, albeit without great confidence, based on the original description: "Fine-grained head sculpture. The forehead has a well-defined frontal depression. The latter has a longitudinal carina, shining, with strongly smoothed grain." Figure 1–5 illustrates a female antenna with four clavomeres.

***Gryon crassifemoratum* Mineo**

Gryon crassifemoratum Mineo, 1990a: 181 (original description. Misspelled *crasifemaratum* in description, abstract; correct spelling (G. Mineo) in title); Johnson, 1992: 381 (cataloged, type information).

Comments. The original description for this species is woefully insufficient. We leave it in *Gryon* based on its placement in the *myrmecophilum* species group (Mineo 1990).

***Gryon crenatum* (Sundholm). comb. nov.**

Figures 41–46; Holotype images: https://www.flickr.com/photos/127240649@N08/50616991701/in/photolist-2k7Rjat-2k7Mx3Y-2k7Rj9M-2k7RTii-2k7Rja8/

Breviscelio crenatus Sundholm, 1970: 383 (original description); Caleca, 1990b: 141 (description); Johnson, 1992: 355 (cataloged, type information); Caleca, 1992: 51, 53 (description, keyed).

***Gryon cultratum* (Kozlov), comb. nov.**
Holotype images: https://zenodo.org/record/5600151#.YXgSFvnMJaQ

Eremioscelio cultratus Kozlov, 1971: 49 (original description); Kozlov, 1972: 656 (keyed); Kozlov, 1978: 622 (description); Kozlov & Kononova, 1990: 311, 312 (description, keyed); Johnson, 1992: 373 (cataloged, type information); Kononova & Kozlov, 2008: 451, 453 (treated as valid species, description, keyed, generic transfer); Timokhov, 2019b: 47 (catalog of species of Russia).

Comments. This synonymy of *Eremioscelio* with *Gryon* implicitly transfers this species. The transfer of *Gryon cultratus* Masner to *Hadronotus* means that homonomy is avoided.

***Gryon cydnoide* (Priesner), comb. rev.**
Figures 29–34; Holotype images in MBD: USNMENT01059665

Hadronotus bernardi Maneval, 1940: (original description); Mineo, 1991: 9 (name considered to be unavailable).

Eremioscelio cydnoides Priesner, 1951: 130 (original description); Kozlov, 1963a: 357 (description); Kozlov, 1963b: 666 (description); Kozlov, 1971: 49 (description); Kozlov, 1972: 656 (keyed); Kozlov, 1978: 62 (description); Mineo & Villa, 1982b: 134 (taxonomic value of structures on the posterior surface of the head); Mineo & Villa, 1982a: 175 (taxonomic value of pleural structures, clypeus, and antennal sensilla); Kozlov & Kononova, 1990: 311 (description, keyed); Johnson, 1992: 373 (cataloged); Notton, 2006: 195 (distribution); Fabritius & Popovici, 2007: 36, 39 (description, keyed); Kononova & Kozlov, 2008: 451, 452 (description, keyed, generic transfer).

Eremioscelio bernardi (Maneval): Masner, 1976: 59 (generic transfer, description); Mineo, 1991: 9 (junior synonym of *Gryon cydnoide* (Priesner)); Johnson, 1992: 373 (cataloged, type information).

Gryon cydnoide (Priesner): Mineo, 1991: 9 (generic transfer, synonymy); Mineo & Caleca, 1994: 126 (distribution); Timokhov, 2019a: 14 (distribution); Timokhov, 2019b: 47 (catalog of species of Russia).

***Gryon delucchii* Mineo & Szabó**
Holotype images: https://zenodo.org/record/4499129#.YBsl3HlOlaQ

Gryon delucchii Mineo & Szabó, 1978a: 88 (original description); Mineo & Gatto, 1981: 187 (description of preimaginal stages); Johnson, 1992: 381 (cataloged, type information); Kononova & Kozlov, 2008: 331, 425 (description, keyed).

Gryon dicaeum (Walker)

Telenomus dicaeus Walker, 1839: 80 (original description).
Microphanurus dicaeus (Walker): Kieffer, 1926: 93, 109 (description, generic transfer, keyed).
Gryon dicaeus (Walker): Masner, 1965: 75 (type information, generic transfer).
Gryon dicaeum (Walker): Johnson, 1992: 381 (cataloged, type information).

Comments. We are unable to determine from the original description if this species belongs in *Hadronotus* or *Gryon* and leave its generic placement unchanged until examination of the type specimen occurs.

Gryon dichropterum Kozlov

Holotype images: https://zenodo.org/record/5600169#.YXgSzfnMJaQ

Gryon dichropterus Kozlov, 1966: 144 (original description); Mineo, 1980a: 191 (description of male); Johnson, 1992: 382 (cataloged, type information).
Eremioscelio dichropterus (Kozlov): Kozlov, 1972: 657 (generic transfer, keyed); Kozlov, 1978: 622 (description); Kozlov & Kononova, 1990: 311, 318 (description, keyed); Kononova & Kozlov, 2008: 452, 458 (description, keyed, generic transfer); Timokhov, 2019b: 47 (catalog of species of Russia).
Gryon dichropterum Kozlov: Mineo & Caleca, 1994: 127, 128 (distribution, keyed).

Gryon dispar Kononova & Petrov

Gryon dispar Kononova & Petrov, 2001: 1479 (original description); Kononova & Petrov, 2002: 57 (keyed); Kononova & Kozlov, 2008: 333, 436 (description, keyed).

Comments. We were not able to determine from the original description if this species belongs in *Gryon* or *Hadronotus*. Its placement thus remains unchanged.

Gryon elatior Masner

Holotype images in MBD: CNC No. 17019

Gryon elatior Masner, 1983: 135, 173 (original description, keyed); Sarazin, 1986: 974 (type information); Johnson, 1992: 382 (cataloged, type information).

Gryon elongatum Mineo, comb. rev.

Holotype images: https://zenodo.org/record/4508091#.YPcj00lKhaQ

Gryon elongatum Mineo, 1991: 22 (original description, assigned to *myrmecophilum* species group); Mineo & Caleca, 1994: 119 (distribution).
Gryon mineoi Özdikmen: Özdikmen, 2011: 772 (replacement name for *Gryon elongatum* Mineo).

Comments. The transfer of *Hadronotus elongatus* Risbec back to *Hadronotus* makes the replacement name no longer necessary for this species.

Gryon eremiogryon Mineo

Gryon eremiogryon Mineo, 1979a: 241 (original description); Mineo, 1979b: 96 (keyed); Johnson, 1992: 382 (cataloged); Kononova & Kozlov, 2008: 333, 440 (description, keyed).

Comments. The original description stated that *G. eremiogryon* has bidentate mandibles and the subsequent discussion expressed Mineo's idea that *G. eremiogryon* was intermediate between *Gryon* and *Eremioscelio*. Given that the latter is now treated as a junior synonym of *Gryon*, we are fairly confident that this species belongs in *Gryon*.

Gryon excertum Kononova & Fursov

Gryon excertus Kononova & Fursov, 2005a: 595 (original description); Kononova & Fursov, 2005b: 304 (description).
Gryon excertum Kononova & Fursov: Kononova & Kozlov, 2008: 329, 409 (description, keyed).

Comments. The original and subsequent descriptions suggest the species should remain in *Gryon*, but it is not entirely clear: "The head sculpture is fine-meshed. Head with short, dense hairs arranged horizontally. The frontal depression above the antennae and the longitudinal frontal carina are absent. Fan-shaped wrinkles on cheeks."

Gryon fasciatum (Priesner)

Figures 73–76; Holotype images in MBD: USNMENT01059667; Images of paratype: https://zenodo.org/record/4837467#.YLExBPlKhaQ

Hadronotus fasciatus Priesner, 1951: 130 (original description); Mineo, 1980b: 214 (type information).
Gryon fasciatus (Priesner): Kozlov, 1978: 619 (description, generic transfer); Kozlov & Kononova, 1989: 81 (keyed); Kozlov & Kononova, 1990: 269, 303 (description, keyed); Kononova & Petrov, 2002: 56 (keyed); Pintureau & al-Nabhan, 2003: 5 (new distribution record from France and Middle East (Syria)); Fabritius & Popovici, 2007: 15, 29 (description, keyed).
Gryon fasciatum (Priesner): Mineo, 1991: 23 (description, assigned to *myrmecophilum* species group); Johnson, 1992: 382 (cataloged, type information); Kononova & Kozlov, 2008: 332, 434 (description, keyed); Timokhov, 2019a: 15 (distribution); Timokhov, 2019b: 47 (catalog of species of Russia).

Gryon firmum Mineo

Holotype images: https://zenodo.org/record/4504446#.YBxseXlOlaQ

Gryon firmum Mineo, 1991: 26 (original description, assigned to *myrmecophilum* species group).

Gryon flaviventre Kononova

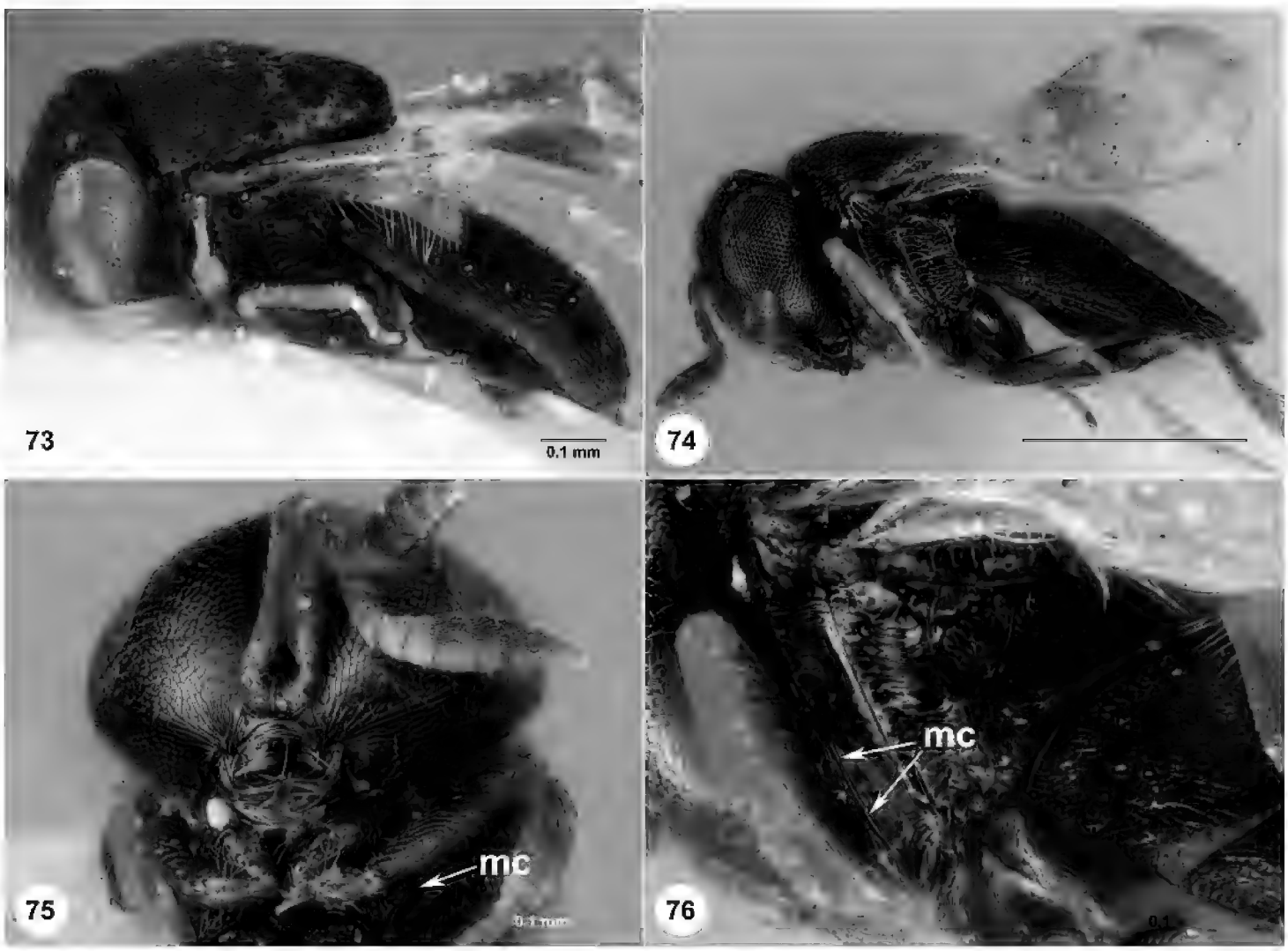
Gryon flaviventris Kononova, 2001: 1469 (original description); Kononova & Petrov, 2002: 53 (keyed); Fabritius & Popovici, 2007: 14, 17 (description, keyed).
Gryon flaviventre Kononova: Kononova & Kozlov, 2008: 323, 345 (description, keyed); Timokhov, 2019b: 47 (catalog of species of Russia).

Comments. This species remains in *Gryon* based on the original description, "The head sculpture is grainy. The frontal depression is weakly expressed, its sculpture is slightly smoothed" and Figure 1–2, which illustrates a female antenna with four clavomeres.

Gryon flavum (Dodd)

Hadronotus flavus Dodd, 1913b: 172 (original description); Dodd, 1915: 18 (keyed); Kieffer, 1926: 455, 469 (description, keyed).
Gryon flavus (Dodd): Galloway, 1976: 91 (type information, generic transfer).
Gryon flavum (Dodd): Johnson, 1992: 383 (cataloged, type information).

Comments. The original description is insufficient for generic placement. We leave this species in *Gryon* and note that the holotype female needs to be examined.



Figures 73–76. *Gryon fasciatum* **73** holotype female (USNMENT01059667), habitus, dorsolateral view **74** paratype female (USNMENT01109130), habitus, lateral view **75** paratype female (USNMENT01109130), head and mesosoma ventral view **76** paratype female (USNMENT01109130), mesosoma, posterolateral view.

Gryon fumosum (Dodd)

Holotype images: https://zenodo.org/record/4504553#.YBxvLHlOlaQ

Hadronotus fumosus Dodd, 1914a: 130 (original description); Dodd, 1915: 20 (keyed); Kieffer, 1926: 455, 472 (description, keyed).
Mirotelenomus fumosus (Dodd): Dodd, 1926: 313 (generic transfer); Galloway, 1976: 109 (type information).
Gryon fumosus (Dodd): Galloway & Austin, 1984: 79 (generic transfer).
Gryon fumosum (Dodd): Mineo, 1990a: 180 (emendation, systematic position); Johnson, 1992: 383 (cataloged, type information).

Gryon fuscum Kononova

Gryon fuscus Kononova, 2001: 1477 (original description); Kononova & Petrov, 2002: 55 (keyed); Fabritius & Popovici, 2007: 29, 68 (keyed).

Gryon rutilator Kononova: Kononova & Kozlov, 2008: 328, 391 (replacement name, description, keyed); Timokhov, 2019b: 48 (catalog of species of Russia).

Comments. The original description lists a few characters that indicate that this species belongs in *Gryon*, "The head sculpture is fine-grained. Frontal depression not shiny, with strongly smoothed grain." *Plastogryon fuscus* Dodd is now treated as a junior synonym of *Hadronotus flavipes*. The replacement name, *Gryon rutilator* Kononova, is thus no longer needed for this species.

Gryon gloriosum Kozlov & Kononova

Gryon gloriosum Kozlov & Kononova, 2004: 200 (original description); Kononova & Kozlov, 2008: 332, 425 (description, keyed).

Comments. We consider it most likely that this species belongs in *Gryon* based on the comparisons to *G. hungaricum* and *G. laetum* in the abstract of the original description.

Gryon goethei (Girault)

Hadronotus goethei Girault, 1932: 5 (original description); Galloway, 1976: 111 (type information, status uncertain); Gordh, Menke, Dahms & Hall, 1979: 297 (reprint of Girault (1932)); Johnson, 1992: 510 (cataloged, type information).

Comments. The description of this species is insufficient for generic placement and examination of the holotype specimen is required.

Gryon gonikopalense Sharma

Figures 77–78; Holotype images in MBD: USNMENT01109129

Gryon gonikopalensis Sharma, 1982: 327, 336 (original description, keyed).
Gryon gonikopalense Sharma: Johnson, 1992: 384 (cataloged).

Gryon gorines Kozlov & Lê

Holotype images in MBD: IEBR 0177

Gryon gorines Kozlov & Lê, 1992: 210, 212, 221 (original description, assigned to *misellum* species group, keyed).

Gryon gorinis Kozlov & Lê, 1996: 10 (description); Lê, 2000: 97, 116 (description, keyed, type information).

Gryon grande Kononova & Petrov

Gryon grandis Kononova & Petrov, 2001: 1476 (original description); Kononova & Petrov, 2002: 55 (keyed).
Gryon grande Kononova & Petrov: Kononova & Kozlov, 2008: 327, 388 (description, keyed).

Comments. This species remains in *Gryon* based on the original description, "Head sculpture fine-grained. Frontal depression shallow, not wide, shining, with distinct longitudinal carina. Frons up to anterior ocellus with fine-grained sculpture" and Figure 2–3 which illustrates a 4-merous clava.

Gryon grownum Kozlov & Lê

Holotype images in MBD: IEBR 0166

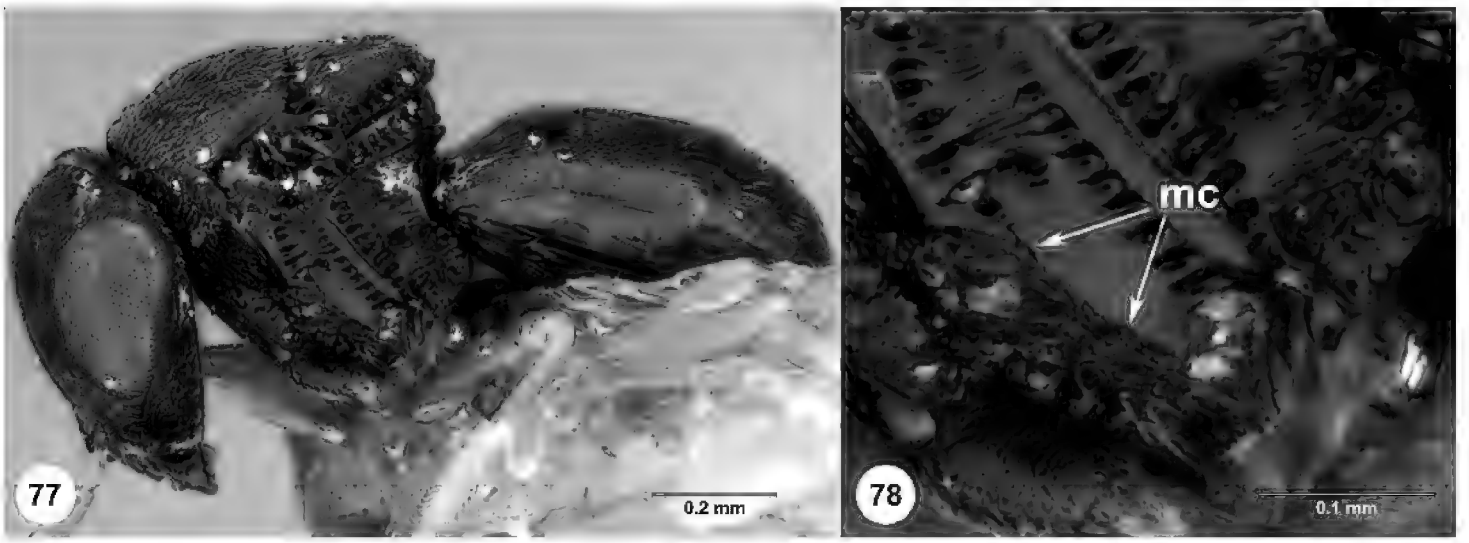
Gryon grownum Kozlov & Lê, 1992: 212, 221 (original description, assigned to *miselum* species group, keyed).
Gryon grownus Kozlov & Lê, 1996: 10 (description); Lê, 2000: 97, 117 (description, keyed, type information).

Gryon gryonis Mineo

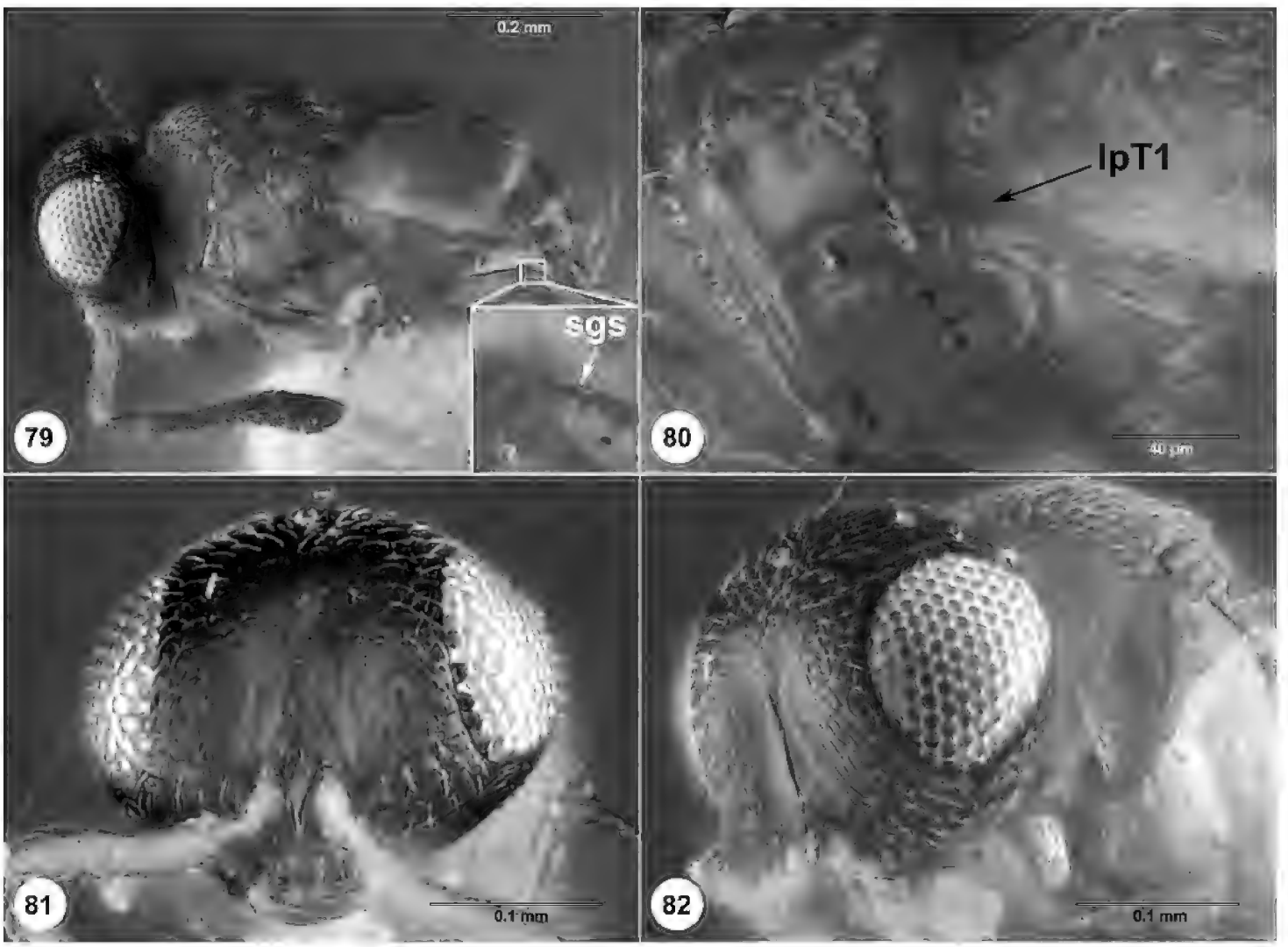
Figures 79–82; Holotype images: https://zenodo.org/record/4504698#.YBx5HXlOlaR

Gryon gryonis Mineo, 1990a: 172 (original description); Johnson, 1992: 384 (cataloged, type information).

Comments. The holotype specimen is very small, only about 0.7 mm in length, and is light in color. This makes it challenging to illustrate and interpret characters with brightfield photography. We believe that this species should remain in *Gryon* based on the apparently 4-merous clava, absence of transverse sculpture in the frontal depression, the glabrous metapleuron that is not dorsoventrally divided by sculpture or setation, and the presence of subgenual spines on the hind tibia (Figures 79–82). The lateral pit on T1 appears to be present but is difficult to discern. The shape of the clypeus and the presence of striation inside the axillar crescent could not be reliably determined from the images of the anterior head and lateral mesosoma, respectively (Figures 79, 81).



Figures 77–78. *Gryon gonikopalense*, holotype female (USNMENT01109129) **77** habitus, lateral view **78** mesosoma, lateral view.



Figures 79–82. *Gryon gryonis*, holotype female **79** habitus, lateral view **80** mesosoma and T1, lateral view **81** head, anterior view **82** head and mesosoma, anterolateral view.

Gryon hospes Kieffer

Plesiobaeus Hospes Kieffer, 1913: 283 (original description).

Plesiobaeus hospes Kieffer: Kieffer, 1926: 556 (description); Masner, 1965: 89 (type information); Kozlov, 1978: 621 (description); Kozlov & Kononova, 1990: 307 (description); Fabritius & Popovici, 2007: 34 (description); Kononova & Kozlov, 2008: 445 (description).

Gryon hospes (Kieffer): Mineo, 1979: 248 (description, generic transfer); Mineo & Caleca, 1987: 53 (description); Johnson, 1992: 384 (cataloged, type information).

Gryon howardi (Mokrzecki & Ogloblin)

Hadronotus howardi Mokrzecki & Ogloblin, 1931: 1 (original description); Masner, 1958: 42 (keyed); Loiácono & Díaz, 1996: 9 (type information).

Hadronotellus howardi (Mokrzecki & Ogloblin): Szabó, 1966: 422, 424 (description of male and female, generic transfer, keyed).

Gryon howardi (Mokrzecki & Ogloblin): Kozlov, 1978: 620 (description, generic transfer); Mineo, 1980a: 193 (description); Kozlov & Kononova, 1989: 78 (keyed); Kozlov & Kononova, 1990: 266, 271 (description, keyed); Johnson, 1992: 384 (cataloged, type information); Mineo & Caleca, 1994: 121 (distribution, assigned to *subfasciatum* group); Kononova & Petrov, 2002: 54 (keyed); Fabritius & Popovici, 2007: 15, 22 (description, keyed); Kononova & Kozlov, 2008: 325, 366 (description, keyed); Timokhov, 2019b: 47 (catalog of species of Russia).

Comments. Figure 3 of the original description clearly illustrates the presence of subgenual spines, confirming that this species belongs in *Gryon*.

Gryon hungaricum (Szabó)

Holotype images: https://zenodo.org/record/4505223#.YByRRXlOlaQ, https://zenodo.org/record/5600192#.YXgTu_nMJaQ

Pannongryon hungaricum Szabó, 1966: 435, 436 (original description, keyed).

Gryon prolongatus Kozlov, 1971: 48 (original description. Synonymized by Mineo (1980a)); Kozlov, 1978: 620 (description); Mineo, 1980a: 196 (junior synonym of *Gryon hungaricum* (Szabó)); Kozlov & Kononova, 1989: 79 (keyed); Kozlov & Kononova, 1990: 267, 287 (description, keyed); Kononova & Petrov, 2002: 53 (keyed); Fabritius & Popovici, 2007: 14, 20 (description, keyed).

Gryon hungaricum (Szabó): Mineo, 1980a: 196 (generic transfer, synonymy); Mineo, 1991: 10, 12 (description, assigned to *hungaricum* species group, keyed); Johnson, 1992: 385 (cataloged, type information); Fabritius & Popovici, 2007: 30 (keyed).

Gryon prolongatum Kozlov: Kononova & Kozlov, 2008: 323, 348 (treated as valid species, keyed).

Comments. Mineo (1980a) treated *G. prolongatum* as a junior synonym of *G. hungaricum* (Szabó). Kononova & Kozlov (2008) recognized the synonymy of *Gryon prolongatus* Kozlov and *Gryon* [*Pannongryon*] *hungaricum* (Szabó) but incorrectly used *G. prolongatum* as the valid name.

***Gryon insidiosum* Mineo**

Holotype images: https://zenodo.org/record/4505396#.YByVHXlOlaQ

Gryon insidiosum Mineo, 1991: 27 (original description, assigned to *myrmecophilum* species group).

***Gryon insulare* (Dodd), comb. nov.**

Holotype images: https://zenodo.org/record/4721645#.YIcRvflKhaQ

Telenomoides insularis Dodd, 1913a: 169, 171 (original description. Preoccupied by *Hadronotus insularis* Ashmead (1894)).

Hadronotus assimilis Dodd: Dodd, 1914a: 129 (replacement name, generic name); Dodd, 1915: 20 (keyed); Kieffer, 1926: 456, 472 (description, keyed).

Mirotelenomus assimilis (Dodd): Dodd, 1926: 313 (generic transfer); Galloway, 1976: 96 (type information); Johnson, 1992: 439 (cataloged, type information).

Gryon assimile (Dodd): Caleca & Mineo, 1995: 19 (generic transfer).

Comments. The 4-merous clava, shape of the clypeus, bidentate mandibles with large teeth, and fine sculpture of the head and dorsal mesosoma are visible in the slide mounted holotype female. Transfer of *Hadronotus insularis* Ashmead from *Gryon* back to *Hadronotus* makes the replacement species name "*assimile*" no longer necessary.

***Gryon investe* (Kieffer)**

Plastogryon investis Kieffer, 1908: 143 (original description. Synonymized by Masner (1961)); Masner, 1961: 160 (junior synonym of *Gryon misellus* Haliday).

Plastogryon Investis Kieffer: Kieffer, 1913: 249 (description).

Plastogryon (*Heterogryon*) *investis* Kieffer: Kieffer, 1926: 446, 449 (description, subgeneric assignment, keyed).

Gryon investis (Kieffer): Kozlov, 1978: 620 (description); Kozlov & Kononova, 1989: 79 (keyed); Kozlov & Kononova, 1990: 267, 277 (description, keyed); Kononova, 1995: 81 (keyed); Kononova & Petrov, 2002: 55 (keyed).

Gryon investe (Kieffer): Kononova & Kozlov, 2008: 326, 377 (treated as valid species, description, keyed); Timokhov, 2019b: 47 (catalog of species of Russia).

Comments. The treatment of *Plastogryon investis* as a junior synonym of *Gryon miselum* by Masner (1961) indicates that, at the least, they are congeneric.

Gryon josephinae Mineo

Holotype images: https://zenodo.org/record/4507012#.YB1W_nlOlaQ

Gryon Josephinae Mineo, 1991: 27 (original description, assigned to *myrmecophilum* species group).
Gryon josephinae Mineo: Mineo & Caleca, 1994: 119 (distribution).

Gryon justum Kozlov & Kononova

Gryon justus Kozlov & Kononova, 1989: 80, 93 (original description, keyed); Kozlov & Kononova, 1990: 268, 291 (description, keyed); Kononova & Petrov, 2002: 55 (keyed).
Gryon justum Kozlov & Kononova: Johnson, 1992: 385 (cataloged, type information); Kononova & Kozlov, 2008: 329, 404 (description, keyed).

Comments. This species remains in *Gryon* based on a character listed in the original description "The frontal impression is deep, not striate."

Gryon kaszabi (Mineo), comb. nov.

Eremioscelio kaszabi Mineo, 1979c: 269 (original description); Johnson, 1992: 373 (cataloged, type information).

Comments. Mineo (1991) transferred *Eremioscelio cydnoides* (type species of *Eremioscelio*) to *Gryon*, implicitly treating *Eremioscelio* as a junior synonym. A few characters in the original description of *E. kaszabi* confirm this placement, "club with four joints", "cheeks and surface of frons...finely, fan-like striate."

Gryon elegans Kononova

Gryon elegans Kononova, 2001: 1478 (original description); Kononova & Petrov, 2002: 56 (keyed); Kononova & Kozlov, 2008: 331, 423 (description, keyed).
Gryon kononovai Özdikmen: Özdikmen, 2011: 771 (replacement name for *Gryon elegans* Kononova).

Comments. The original description provides some evidence for leaving this species in *Gryon*, "The head sculpture is fine-grained, resembles fine emery." Our transfer of

Plastogryon elegans Dodd to *Hadronotus* eliminates the need for the replacement name *Gryon kononovai*.

Gryon lada Kozlov

Holotype images: https://zenodo.org/record/5600220#.YXgUgfnMJaQ

Gryon lada Kozlov, 1972: 651 (original description); Kozlov & Kononova, 1989: 81 (keyed); Kozlov & Kononova, 1990: 269, 305 (description, keyed); Johnson, 1992: 386 (cataloged, type information); Kononova, 1995: 81 (keyed); Kononova & Petrov, 2002: 57 (keyed); Kononova & Kozlov, 2008: 333, 438 (description, keyed).

Gryon laetum Kozlov & Kononova

Gryon laetum Kozlov & Kononova, 2004: 201 (original description); Kononova & Kozlov, 2008: 332, 432 (description, keyed).

Comments. Figure 1–4 in the original description matches the distinct habitus found in many species of *Gryon* (e.g., *G. myrmecophilum*) and illustrates a striate interior of the axillula, which is a diagnostic character for the genus.

Gryon lala Kozlov

Holotype images: https://zenodo.org/record/5600277#.YXgWBvnMJaQ

Gryon lala Kozlov, 1972: 652 (original description); Mineo, 1980a: 197 (systematic relationships); Kozlov & Kononova, 1989: 79 (keyed); Kozlov & Kononova, 1990: 267, 288 (description, keyed); Johnson, 1992: 386 (cataloged, type information); Kononova, 1995: 84 (keyed); Kononova & Petrov, 2002: 54 (keyed); Fabritius & Popovici, 2007: 26, 66 (keyed); Kononova & Kozlov, 2008: 326, 376 (description, keyed).

Gryon lamia (Kozlov), comb. nov.

Holotype images: https://zenodo.org/record/5600383#.YXgYLfnMJaQ

Eremioscelio lamia Kozlov, 1972: 655, 656 (original description, keyed); Kozlov & Kononova, 1990: 311, 315 (description, keyed); Johnson, 1992: 373 (cataloged, type information); Kononova, 1995: 85 (keyed); Kononova & Kozlov, 2008: 452, 455 (description, keyed, generic transfer); Timokhov, 2019b: 47 (catalog of species of Russia).

***Gryon largi* (Ashmead)**
Lectotype images in MBD: USNMENT00989858

Hadronotus largi Ashmead, 1893: 230, 231 (original description); Brues, 1910: 47 (keyed); Kieffer, 1926: 454, 462 (description, keyed).
Gryon largi (Ashmead): Muesebeck & Masner, 1967: 299 (generic transfer); Masner & Muesebeck, 1968: 35 (lectotype designation); Masner, 1983: 135, 169 (description, keyed); Johnson, 1992: 386 (cataloged, type information).

***Gryon latum* (Kozlov), comb. rev.**
Holotype images: https://zenodo.org/record/5600360#.YXgXB_nMJaQ

Mirotelenomus latus Kozlov, 1963a: 356 (English translation of original description, keyed); Kozlov, 1963b: 664 (original description, keyed, preoccupied by *Austroscelio latus* Dodd, 1916); Kozlov, 1978: 621 (description); Johnson, 1992: 392 (type information).
Gryon latus (Kozlov): Mineo, 1979a: 255 (generic transfer).
Exon latus (Kozlov): Masner, 1980: 22 (generic transfer); Kozlov & Kononova, 1990: 308, 309 (description, keyed); Kononova & Petrov, 2002: 57 (keyed).
Gryon latum (Kozlov): Mineo & Caleca, 1987b: 49, 50 (diagnosis, keyed).
Gryon kozlovi Mineo: Mineo, 1990a: 171 (unnecessarily proposed replacement name).
Exon latum (Kozlov): Kononova & Kozlov, 2008: 447 (description, keyed, generic transfer).

Comments. Our treatment of *Exon* as a junior synonym of *Gryon* implicitly transfers this species.

***Gryon lena* Kozlov**
Holotype images: https://zenodo.org/record/5600372#.YXgXmvnMJaQ

Gryon lena Kozlov, 1972: 655 (original description); Kozlov & Kononova, 1989: 80 (keyed); Kozlov & Kononova, 1990: 268, 289 (description, keyed); Johnson, 1992: 386 (cataloged, type information); Kononova & Petrov, 2002: 55 (keyed); Kononova & Kozlov, 2008: 328, 398 (description, keyed).

Comments. This species remains in *Gryon* based on the redescription in Kozlov & Kononova (1990): "The frontal depression above the antennae is deep, with finely sculpted sculpture. The head sculpture is fine-grained." However, we consider it necessary for the holotype specimen to be examined for confident placement.

Gryon longipenne (Dodd)

Platyteleia longipennis Dodd, 1913c: 335 (original description); Kieffer, 1926: 409 (description, keyed); Galloway, 1976: 101 (type information).
Gryon longipennis (Dodd): Galloway & Austin, 1984: 79 (generic transfer).
Gryon longipenne (Dodd): Mineo, 1990b: 58 (type information); Johnson, 1992: 387 (cataloged, type information).

Comments. Generic placement cannot be determined from the original description and examination of the holotype is needed.

Gryon lymantriae (Masner), comb. rev.

Hadronotus lymantriae Masner, 1958: 39, 42 (original description, keyed).
Gryon lymantriae (Masner): Masner, 1965: 77 (type information, generic transfer); Mineo, 1979a: 257 (description); Johnson, 1992: 387 (cataloged, type information); Mineo & Caleca, 1994: 127, 128 (distribution, keyed, synonymy).
Masneria lymantriae (Masner): Szabó, 1966: 442 (description of male and female, generic transfer).
Eremioscelio lymantriae (Masner): Kozlov, 1972: 657 (generic transfer, keyed); Kozlov, 1978: 622 (description); Livshits & Kuslitskii, 1989: 49 (keyed); Kozlov & Kononova, 1990: 311, 316 (description, keyed); Fabritius & Popovici, 2007: 36 (description, keyed); Kononova & Kozlov, 2008: 452, 456 (description, keyed, generic transfer); Timokhov, 2019b: 47 (catalog of species of Russia).

Gryon maculatum Kozlov & Kononova

Gryon maculatum Kozlov & Kononova, 2004: 201 (original description); Kononova & Kozlov, 2008: 328, 400 (description, keyed); Timokhov, 2019b: 47 (catalog of species of Russia).

Comments. The original description suggests that this species belongs in *Gryon*, but is not entirely clear, "The head is fine-grained. The second impression is distinct, with a longitudinal carina, in fine-grained ornamentation."

Gryon magnum Kozlov & Kononova

Gryon magnus Kozlov & Kononova, 1989: 81, 99 (original description, keyed); Kozlov & Kononova, 1990: 269, 304 (description, keyed); Kononova & Petrov, 2002: 57 (keyed).

Gryon magnum Kozlov & Kononova: Johnson, 1992: 388 (cataloged, type information); Kononova & Kozlov, 2008: 333, 436 (description, keyed).

Comments. This species remains in *Gryon* based on the original description: "The frontal depression is shallow, with finer, significantly smoothed granularity. The forehead and the vertex are coarse-grained."

Gryon marina Kozlov & Kononova

Gryon marina Kozlov & Kononova, 1989: 81, 97 (original description, keyed); Kozlov & Kononova, 1990: 269, 301 (description, keyed); Johnson, 1992: 388 (cataloged, type information); Kononova, 1995: 85 (keyed); Kononova & Petrov, 2002: 56 (keyed); Kononova & Kozlov, 2008: 332, 433 (description, keyed); Timokhov, 2019b: 47 (catalog of species of Russia).

Comments. We consider it best to leave this species in *Gryon* based on characters in the original description, "The head is finely meshed" and "Cheeks from above in thin longitudinal wrinkles."

Gryon medium Kononova & Petrov

Gryon medius Kononova & Petrov, 2001: 1476 (original description); Kononova & Petrov, 2002: 55 (keyed).
Gryon medium Kononova & Petrov: Kononova & Kozlov, 2008: 327, 386 (description, keyed).

Comments. The original description illustrates a female antenna with four clavomeres and describes the sculpture of the frontal depression as "smoothed."

Gryon menthes Kozlov & Lê

Holotype images in MBD: ZIN 0092; Paratype images in MBD: USNMENT01223670

Gryon menthes Kozlov & Lê, 1992: 220, 221 (original description, assigned to *misellum* species group, keyed).
Gryon menthis Kozlov & Lê, 1996: 9 (description); Lê, 2000: 96, 123 (description, keyed, type information).

Comments. Images of the paratype specimens show the presence of striation of the axillula and the lateral pit on T1.

Gryon micropterum (Kieffer)

Hadronotus brevipennis Kieffer, 1909: 270 (original description. Preoccupied by *Hadronotus brevipennis* Harrington (1900)).
Hadronotus Micropterus (Kieffer): Kieffer, 1913: 244 (replacement name).
Hadronotus micropterus (Kieffer): Kieffer, 1926: 453, 457 (description, keyed); Bin, 1974: 455 (type information).
Gryon micropterus (Kieffer): Johnson, 1992: 388 (cataloged, type information).

Comments. The original description is insufficient for generic placement. We leave this species in its current placement until the holotype can be examined.

Gryon minutum Mineo

Holotype images: https://zenodo.org/record/4508843#.YJLuMaEpBaQ

Gryon minimum Mineo, 1990a: 173 (original description. Preoccupied by *Hadronotus minimus* Kieffer (1908)); Johnson, 1992: 388 (cataloged, type information).
Gryon minutum Mineo: Mineo, 1991: 7 (replacement name for *Gryon minimum* Mineo, assigned to *artum* species group).

Gryon minimum (Kieffer)

Hadronotus minimus Kieffer, 1908: 35 (original description); Kieffer, 1926: 455, 467 (description, keyed).
Gryon minimus (Kieffer): Alayo Dalmau, 1973: 99 (cataloged).
Gryon minimum (Kieffer): Johnson, 1992: 388 (cataloged).

Comments. The original description suggests that this species belongs in *Gryon* and so we leave it here for now, albeit without great confidence: "head wider than thorax, slightly arched back, twice as wide as long, smooth and shiny on the front which gives an unlimited frontal impression, finely chagrined on the rest."

Gryon mirum Kononova & Petrov

Gryon mirus Kononova & Petrov, 2001: 1477 (original description); Kononova & Petrov, 2002: 55 (keyed).
Gryon mirum Kononova & Petrov: Kononova & Kozlov, 2008: 327, 389 (description, keyed).

Comments. This species remains in *Gryon* based on the original description, "frontal impression with granular, strongly smoothed sculpture, shining."

Gryon misellum Haliday

Figures 21–25; Lectotype images: https://zenodo.org/record/4498847#.YB2OJmFKhaQ
Paralectotype images: https://zenodo.org/record/4724052#.YIh-SPlKhaQ

Gryon misellum Haliday, 1833: 271 (original description, keyed); Kieffer, 1926: 261 (description, keyed); Mineo, 1980a: 197 (variation); Masner, 1983: 135, 165 (description, keyed); Mineo & Caleca, 1987b: 44 (taxonomic status of Nearctic specimens); Mineo, 1990: 54 (distribution); Johnson, 1992: 388 (cataloged, type information); Mineo & Caleca, 1994: 120 (distribution); Pintureau & al-Nabhan, 2003: 2 (description, new distribution record from Portugal and France); Kononova & Kozlov, 2008: 326, 378 (description, keyed); Timokhov, 2019b: 47 (catalog of species of Russia).

Teleas pumilio Nees von Esenbeck, 1834: 288 (original description. Synonymized by Masner (1961)); Dalla Torre, 1898: 519 (generic transfer); Masner, 1961: 160 (junior synonym of *Gryon misellus* Haliday).

Gryon misellus Haliday: Walker, 1836: 344 (description, emendation); Kieffer, 1908: 190 (description); Masner, 1961: 160 (description, synonymy, lectotype designation); Kozlov, 1963a: 357, 358 (description, keyed); Kozlov, 1963b: 667 (description, keyed); Hellén, 1971: 21 (description); Kozlov, 1978: 620 (description); Kozlov & Kononova, 1989: 79 (keyed); Kozlov & Kononova, 1990: 267, 278 (description, keyed); Kononova, 1995: 81 (keyed); Kononova & Petrov, 2002: 55 (keyed); Fabritius & Popovici, 2007: 15, 26 (description, keyed).

Teleas misellus (Haliday): Blanchard, 1840: 290 (description, generic transfer).

Telenomus divisus Wollaston, 1858: 25 (original description. Synonymized by Graham (1984)); Kieffer, 1926: 39 (description); Johnson, 1992: 388 (type information).

Acolus basalis Thomson, 1859: 422 (original description. Synonymized by Masner (1961)); Masner, 1961: 160 (junior synonym of *Gryon misellus* Haliday).

Acolus opacus Thomson, 1859: 422 (original description. Synonymized by Masner (1961)); Masner, 1961: 160 (junior synonym of *Gryon misellus* Haliday).

Gryon pumilio (Nees von Esenbeck): Mayr, 1879: 698 (generic transfer).

Plastogryon Försteri Kieffer, 1908: 141 (original description. Synonymized by Masner (1961)); Kieffer, 1913: 246 (description); Masner, 1961: 160 (junior synonym of *Gryon misellus* Haliday).

Plastogryon pumilio (Nees von Esenbeck): Kieffer, 1908: 144 (generic transfer).

Plastogryon sagax Kieffer, 1908: 142 (original description. Synonymized by Masner (1961)); Masner, 1961: 160 (junior synonym of *Gryon misellus* Haliday).

Plastogryon sagax var. *brevipennis* Kieffer, 1908: 143 (original description. Synonymized by Masner (1961)); Masner, 1961: 160 (junior synonym of *Gryon misellus* Haliday).

Acoloides basalis (Thomson): Brues, 1908: 17 (diagnosis, list of species).

Acoloides opacus (Thomson): Brues, 1908: 17 (diagnosis, list of species).

Paragryon ? *Misellus* (Haliday): Kieffer, 1910: 99 (generic transfer).

Holacolus Basalis (Thomson): Kieffer, 1912: 107 (description, generic transfer).

Holacolus Opacus (Thomson): Kieffer, 1912: 107 (description, generic transfer).

Gryon Misellus Haliday: Kieffer, 1913: 214 (description).

Gryon Walkeri Kieffer, 1913: 216 (original description. Synonymized by Masner (1961)); Masner, 1961: 160 (junior synonym of *Gryon misellus* Haliday).
Plastogryon Brevipennis Kieffer: Kieffer, 1913: 247 (description).
Plastogryon Pumilio (Nees von Esenbeck): Kieffer, 1913: 247 (description).
Plastogryon Sagax Kieffer: Kieffer, 1913: 249 (description).
Hadronotus divisus (Wollaston): Dodd, 1920a: 351 (generic transfer).
Gryon walkeri Kieffer: Kieffer, 1926: 261, 262 (description, keyed).
Holacolus basalis (Thomson): Kieffer, 1926: 170 (description, keyed).
Holacolus opacus (Thomson): Kieffer, 1926: 170 (description, keyed).
Plastogryon (*Heterogryon*) *brevipennis* Kieffer: Kieffer, 1926: 446, 448 (description, subgeneric assignment, keyed).
Plastogryon (*Heterogryon*) *pumilio* (Nees von Esenbeck): Kieffer, 1926: 446, 449 (description, subgeneric assignment, keyed).
Plastogryon (*Heterogryon*) *sagax* Kieffer: Kieffer, 1926: 446, 448 (description, subgeneric assignment, keyed).
Plastogryon (*Plastogryon*) *foersteri* Kieffer: Kieffer, 1926: 446, 447 (description, subgeneric assignment, keyed).
Gryon divisus (Wollaston): Masner, 1965: 75 (type information, generic transfer).
Gyron misellum Haliday: O'Connor, Nash, Notton & Fergusson, 2004: 25 (misspelling, catalog of Irish species).

***Gryon moczari* (Szabó), comb. nov.**
Figures 35–40; Holotype images in MBD: Hym.Typ.No. 9634, Mus.Budapest

Hungarogryon moczari Szabó, 1966: 443 (original description); Kozlov, 1978: 621 (description); Mineo, 1979: 261 (figure); Kozlov & Kononova, 1990: 320 (keyed); Johnson, 1992: 402 (cataloged, type information); Mineo, 2005: 34 (new distribution record, host presumption); Kononova & Kozlov, 2008: 462 (description).

Comments. See generic synonymy.

***Gryon monspeliense* (Picard)**
Holotype images: https://zenodo.org/record/4509056#.YB2PYGFKhaQ
Lectotype images: https://zenodo.org/record/5600406#.YXgZFPnMJaQ

Hadronotus monspeliensis Picard, 1924: 107 (original description).
Hadronotus afanasievi Meier, 1949: (original description. reference from Kozlov (1963c). Synonymized by Kozlov (1978)).
Hadronotus afanassievi Meier: Ryakhovskii, 1959: 81 (description).
Hadronotus telengai Ryakhovskii, 1959: 81, 84 (original description, keyed. Synonymized by Kozlov (1963c)); Kozlov, 1963c: 295 (junior synonym of *Gryon afanasievi* (Meier)); Johnson, 1992: 389 (type information).

Gryon afanasievi (Meier): Kozlov, 1963c: 295, 296 (description).
Hadronotellus monspeliensis (Picard): Szabó, 1966: 423, 427 (description, generic transfer, keyed).
Gryon monspeliensis (Picard): Mineo, 1977: 82 (description of preimaginal stages); Kozlov, 1978: 619 (description, generic transfer); Mineo, 1979a: 258 (type information); Mineo, 1979b: 94 (keyed); Kozlov & Kononova, 1989: 80 (keyed); Kozlov & Kononova, 1990: 268, 299 (description, keyed); Kononova & Petrov, 2002: 56 (keyed); Fabritius & Popovici, 2007: 16, 32 (description, keyed); Timokhov, 2019b: 47 (catalog of species of Russia).
Gryon laraichii Mineo: Mineo, 1979b: 94 (original description, keyed); Mineo, 1979a: 255 (description); Johnson, 1992: 386 (cataloged, type information); Mineo & Caleca, 1994: 121 (distribution, assigned to *subfasciatum* group); Kononova & Kozlov, 2008: 429 (junior synonym of *Gryon monspeliense* (Picard)).
Gryon monspeliense (Picard): Johnson, 1992: 389 (cataloged, type information); Mineo & Caleca, 1994: 121 (distribution, assigned to *subfasciatum* group); Kononova & Kozlov, 2008: 332, 429 (description, keyed, synonymy).

Gryon montanum (Kieffer)

Hadronotus montanus Kieffer, 1906: 5 (original description).
Hadronotus? *montanus* Kieffer: Kieffer, 1908: 145 (redescribed as new).
Psiloteleia montanus (Kieffer): Kieffer, 1926: 452 (description, keyed).
Gryon montanus (Kieffer): Mani & Sharma, 1982: 192 (generic transfer).
Gryon montanum (Kieffer): Johnson, 1992: 390 (cataloged).

Comments. Generic placement cannot be made from the original description. We leave this species in its current designation until the holotype specimen can be examined.

Gryon muscorum Kozlov & Kononova

Gryon muscorum Kozlov & Kononova, 2004: 202 (original description); Kononova & Kozlov, 2008: 327, 380 (description, keyed).

Comments. We were unable to determine the generic placement of this species, and thus it remains in *Gryon* until the holotype specimen can be examined.

Gryon myrmecophilum (Ashmead)

Holotype images in MBD: USNMENT00989861

Hadronotus myrmecophilus Ashmead, 1893: 230, 232 (original description, keyed); Brues, 1910: 47 (keyed); Kieffer, 1926: 454, 462 (description, keyed).

Gryon myrmecophilus (Ashmead): Muesebeck & Masner, 1967: 299 (generic transfer); Masner & Muesebeck, 1968: 36 (type information).
Gryon myrmecophilum (Ashmead): Masner, 1983: 135, 170 (description, emendation, keyed); Johnson, 1992: 390 (cataloged, type information).

***Gryon nigriceps* (Dodd)**
Holotype images: https://zenodo.org/record/4509346#.YB2ZMHlOlaQ

Hadronotus nigriceps Dodd, 1914b: 81 (original description); Dodd, 1915: 19 (keyed); Kieffer, 1926: 455, 469 (description, keyed).
Mirotelenomus nigriceps (Dodd): Dodd, 1926: 313 (generic transfer); Galloway, 1976: 109 (type information).
Gryon nigriceps (Dodd): Galloway & Austin, 1984: 79 (generic transfer); Johnson, 1992: 391 (cataloged, type information).

Comments. The head of the holotype male is slide-mounted and crushed. However, the distinctive shape of the clypeus found in *Gryon* and facial striae are visible on both sides of the head. The image of the dorsal meso- and metasoma shows the carina on T1 that is directly medial to the lateral pit that is diagnostic for *Gryon*, although the pit itself is not visible. This image also appears to show a subgenual spine on the right tibia.

***Gryon nitens* (Szabó)**
Holotype images in MBD: Hym.Typ.No. 9630, Mus.Budapest

Sundholmia nitens Szabó, 1966: 439 (original description. Synonymized by Mineo & Caleca (1987b)).
Gryon nitens (Szabó): Mineo, 1980a: 200 (generic transfer, description); Johnson, 1992: 392 (cataloged, type information).

Comments. Most of the diagnostic characters that place this species in *Gryon* are visible in the holotype but the specimen is not entirely clean. In lateral view, the subgenual spines are apparent and the metapleuron is not dorsoventrally divided by a change in sculpture or setation. In dorsal view, the striation is visible in the anterior portion of the axillar crescent and the foveae along the anterior margin of T1 are uniform in size, ending sublaterally in a carina. The lateral pit on T1 is obscured. The anterolateral view of the head illustrates that the frons does not have macrosculpture.

***Gryon nosulcum* Kozlov & Lê**
Holotype images in MBD: IEBR 0173

Gryon nosulcum Kozlov & Lê, 1992: 212, 221 (original description, assigned to *miselum* species group, keyed).
Gryon nosulcus Kozlov & Lê, 1996: 10 (description); Lê, 2000: 97, 128 (description, keyed, type information).

Gryon obscurum Mineo

Holotype images: https://zenodo.org/record/4509680#.YB2-UXlOlaQ

Gryon obscurum Mineo, 1991: 27 (original description, assigned to *myrmecophilum* species group).

Gryon oligomerum Kononova

Paratype images: https://zenodo.org/record/5176809#.YRK9lcpKhaQ

Gryon oligomerum Kononova: Kononova, Pavlicek & Nevo, 2005: 816 (description); Kononova, Pavlicek & Nevo, 2005: 1358 (original description); Kononova & Kozlov, 2008: 329, 406 (description, keyed).

Comments. Figures 6–1 and 6–2 in the original description illustrate the anterior head and the female antenna, both of which indicate that this species belongs in *Gryon*. The holotype specimen is mounted in a way that prevents observation of the lateral mesosoma (Cristina Vasiliţa, personal communication), but the presence of a complete mesopleural carina is visible on some of the paratype specimens, which have identical collection data. Also, in the paratype specimen photographed, the acetabular carina and ventral mesopleural carina do not intersect ventrally, providing another character by which this species may be separated from *G. aetherium*. The medial infuscation of the fore wing, illustrated in Figure 5–1 of the original description, is similar to that of *G. fasciatum*, which was described from Egypt. Because *G. oligomerum* was described from Israel, these species should be compared in future work.

Gryon paradigma Mineo

Figures 26–28; Holotype images: https://zenodo.org/record/4519703#.YCFmDXlOlaQ

Gryon paradigma Mineo, 1991: 29 (original description, assigned to *myrmecophilum* species group).

Comments. Females of this species have 11 antennomeres. Figure 12 in the original description illustrates this and the number of antennomeres can also be counted in the images of the holotype specimen. However, in the original description Mineo (1991)

stated, "Female... antenna, excluding A9-A12 brown," indicating that he might not have been aware of this antennal character.

***Gryon parafasciatum* Mineo**
Holotype images: https://zenodo.org/record/4519716#.YCFn53lOlaQ

Gryon parafasciatum Mineo, 1991: 30 (original description, assigned to *myrmecophilum* species group).

***Gryon parkeri* (Fouts)**
Holotype images in MBD: USNMENT00989862

Hadronotus parkeri Fouts, 1920: 64 (original description).
Gryon parkeri (Fouts): Muesebeck & Masner, 1967: 299 (generic transfer); Masner & Muesebeck, 1968: 36 (type information); Masner, 1983: 135, 167 (description, keyed); Johnson, 1992: 393 (cataloged, type information).

***Gryon patroclus* Mineo**
Holotype images: https://zenodo.org/record/4519784#.YCFq_XlOlaQ

Gryon patroclus Mineo, 1994: 119 (original description, assigned to *myrmecophilum* group).

***Gryon pedestre* (Nees von Esenbeck)**
Syntype images in MBD: ZMUC 0002

Teleas pedestris Nees von Esenbeck, 1834: 293 (original description); Graham, 1988: 33 (publication of drawing by Westwood of Nees's specimen, generic transfer. This change in interpretation of *Teleas pedestris* may negate some or all of the reported synonymies).
Platygaster apterus Nees von Esenbeck, 1834: 299 (original description); Kononova & Kozlov, 2001: 284 (junior synonym of *Trimorus pedestris* (Nees von Esenbeck)).
Prosacantha pedestris (Nees von Esenbeck): Thomson, 1859: 431 (description, generic transfer).
Prosacantha subtilis Thomson, 1859: 430 (original description. Synonymized by Szabó (1966)); Szabó, 1966: 46 (junior synonym of *Trimorus pedestris* (Nees von Esenbeck)); Johnson, 1992: 393 (type information).
Hoplogryon Subtilis (Thomson): Kieffer, 1908: 210 (generic transfer, keyed).
Hoplogryon pedestris (Nees von Esenbeck): Kieffer, 1908: 202, 212 (generic transfer, keyed).

Hoplogryon (*Hoplogryon*) *pedestris* (Nees von Esenbeck): Kieffer, 1910: 97 (subgeneric assignment); Kieffer, 1926: 183, 186, 189 (description, keyed).
Hoplogryon (*Hoplogryon*) *subtilis* (Thomson): Kieffer, 1910: 98 (subgeneric assignment); Kieffer, 1926: 186, 201 (description, keyed).
Hoplogryon Pedestris (Nees von Esenbeck): Kieffer, 1912: 114, 151 (description).
Hoplogryon subtilis (Thomson): Kieffer, 1912: 144 (description).
Hadronotellus pedester Kieffer, 1917: 341 (original description); Szabó, 1966: 423, 425 (description, type information, keyed); Hellén, 1971: 23 (description).
Hadronotus pedester (Kieffer): Kieffer, 1926: 453, 456 (generic transfer, description, keyed); Meier, 1940: 80 (description, keyed); Ryakhovskii, 1959: 81 (keyed).
Platygaster aptera Nees von Esenbeck: Kieffer, 1926: 826 (description, emendation); Vlug, 1995: 48 (cataloged).
Trimorus pedestris (Nees von Esenbeck): Szabó, 1966: 25, 46 (description, synonymy, keyed); Fabritius, 1969: 271 (description); Kozlov, 1978: 625 (description); Kononova & Kozlov, 2001: 160, 165, 284 (description, keyed, no mention of generic transfer by Graham (1988), synonymy).
Trimorus subtilis (Thomson): Sundholm, 1967: 133 (lectotype designation, generic transfer).
Gryon pedester (Kieffer): Mineo, 1979b: 96 (keyed).
Gryon pedestre (Nees von Esenbeck): Johnson, 1992: 393 (cataloged); Johnson, 1992: 394 (cataloged, type information); Mineo & Caleca, 1994: 121 (distribution, assigned to *subfasciatum* group); Buhl, 1997: 42 (description); Fabritius & Popovici, 2007: 14, 18 (description, keyed).
Gryon krygeri Buhl: Buhl, 1997: 41 (replacement name for *Hadronotellus pedester* Kieffer, preoccupied by *Teleas pedestris* Nees von Esenbeck, junior synonym of *Gryon pedestre* (Nees von Esenbeck)).

***Gryon pisus* (Nixon)**
Holotype images: https://zenodo.org/record/4520662#.YCGHVXlOlaQ

Hadronotus pisus Nixon, 1934b: 292, 297 (original description, keyed); Risbec, 1950: 592, 593, 638 (description, variation, keyed).
Hadronotus Basilewskyi Risbec, 1957: 140 (original description).
Gryon pisus (Nixon): Masner, 1965: 78 (type information, generic transfer).
Gryon basilewskyi (Risbec): Masner, 1976: 58 (generic transfer, systematic position); Johnson, 1992: 379 (cataloged, type information).
Gryon pisum (Nixon): Mineo, 1991: 32 (emendation, description, synonymy, assigned to *myrmecophilum* species group); Johnson, 1992: 394 (cataloged, type information).
Hadronotus basilewskyi Risbec: Mineo, 1991: 32 (junior synonym of *Gryon pisum* (Nixon)).

Comments. This species was named after Pisus, son of Aphraeus, a character from Greek mythology, and thus the species epithet should be treated as an appositional noun.

Gryon politum (Ashmead)

Hadronotus politus Ashmead, 1894: 229, 230 (original description, keyed); Ashmead, 1900: 328 (distribution); Kieffer, 1926: 455, 466 (description, keyed).
Gryon politus (Ashmead): Masner, 1976: 58 (generic transfer, type information).
Gryon politum (Ashmead): Johnson, 1992: 394 (cataloged, type information).

Comments. The original description is insufficient for placing this species, and we leave it under its current generic assignment.

Gryon prisma Mineo

Holotype images: https://zenodo.org/record/4520676#.YCGH7HlOlaQ

Gryon prisma Mineo, 1991: 34 (original description, assigned to *myrmecophilum* species group); Mineo & Caleca, 1994: 120 (distribution).

Gryon psilantere Kozlov & Lê

Holotype images in MBD: IEBR 0174

Gryon psilantere Kozlov & Lê, 1992: 213, 221 (original description, assigned to *miselum* species group, keyed).
Gryon psilanteris Kozlov & Lê, 1996: 10 (description); Lê, 2000: 97, 130 (description, keyed, type information).

Gryon rectum Kozlov & Kononova

Gryon rectus Kozlov & Kononova, 1989: 80, 95 (original description, keyed); Kozlov & Kononova, 1990: 268, 297 (description, keyed); Kononova & Petrov, 2002: 56 (keyed); Fabritius & Popovici, 2007: 16, 31 (description, keyed).
Gryon rectum Kozlov & Kononova: Johnson, 1992: 395 (cataloged, type information); Kononova & Kozlov, 2008: 332, 427 (description, keyed).

Comments. The original description does not list any characters that would exclude this species from *Gryon*, but confident determination will require examination of the holotype.

Gryon regulare Kozlov & Kononova

Gryon regularis Kozlov & Kononova, 1989: 80, 92 (original description, keyed); Kozlov & Kononova, 1990: 268, 290 (description, keyed); Kononova & Petrov, 2002: 55 (keyed).

Gryon regulare Kozlov & Kononova: Johnson, 1992: 395 (cataloged, type information); Kononova & Kozlov, 2008: 329, 401 (description, keyed).

Comments. The original description is consistent with placement of this species in *Gryon*, especially the following "Cheeks from above are thinly striated longitudinally". However, examination of the type specimen is needed.

Gryon remotum Mineo

Holotype images: https://zenodo.org/record/4520735#.YCGJ53lOlaQ

Gryon remotum Mineo, 1991: 35 (original description, assigned to myrmecophilum species group).

Gryon rubrigaster (Szabó)

Holotype images: https://zenodo.org/record/4521199#.YCGeenlOlaQ

Pannongryon rubrigaster Szabó, 1966: 435, 437 (original description, keyed).
Gryon rubrigaster (Szabó): Mineo, 1979a: 261 (generic transfer, type information); Mineo & Szabó, 1979: 272 (description of male); Mineo, 1991: 36 (description, assigned to *myrmecophilum* species group); Johnson, 1992: 395 (cataloged, type information); Mineo & Caleca, 1994: 120 (distribution); Kononova & Kozlov, 2008: 322, 338 (description, keyed).

Gryon rubrum Kononova & Petrov

Gryon rubrum Kononova & Petrov, 2001: 1470 (original description); Kononova & Petrov, 2002: 53 (keyed); Kononova & Kozlov, 2008: 323, 346 (description, keyed).

Comments. The original description refers to the head sculpture as "fine-grained, strongly smoothed" and provides no characters that would lead us to remove it from *Gryon*.

Gryon rubtzovi (Ryakhovskii)

Lectotype images: https://zenodo.org/record/5600418#.YXgZ4vnMJaQ

Hadronotus rubtzovi Ryakhovskii, 1959: 81 (original description).
Gryon rubtzovi (Ryakhovskii): Kozlov, 1963a: 358 (description, generic transfer, lectotype designation, keyed); Kozlov, 1963b: 667, 668 (description, keyed, generic transfer, lectotype designation); Johnson, 1992: 395 (cataloged, type information); Mineo & Caleca, 1994: 127 (junior synonym of *Gryon lymantriae* (Masner)); Kon-

onova & Petrov, 2002: 55 (keyed); Kononova & Kozlov, 2008: 328, 392 (treated as valid species, description, keyed, synonymy).

Gryon rubtzovi Kozlov & Kononova, 1989: 78, 86 (original description, keyed. An objective junior synonym of *Hadronotus rubtzovi* Ryakhovskii (1959)); Kozlov & Kononova, 1990: 266, 275 (description, keyed); Johnson, 1992: 395 (cataloged, type information); Kononova & Kozlov, 2008: 392 (implicitly synonymized with *Gryon rubtzovi* (Ryakhovskii)).

Gryon rufescens Kozlov & Kononova

Gryon rufescens Kozlov & Kononova, 2004: 206 (original description); Kononova & Kozlov, 2008: 328, 393 (description, keyed); Timokhov, 2019b: 48 (catalog of species of Russia).

Comments. Our translation of the original description, and the illustrations provided therein, are not sufficient for us to determine the generic placement of this species. Therefore, we leave it in *Gryon*.

Gryon simile Kozlov & Kononova

Holotype images: https://zenodo.org/record/4532038#.YCQxiHlOlaQ

Gryon similis Kozlov & Kononova, 1989: 79, 88 (original description, keyed); Kozlov & Kononova, 1990: 267, 279 (description, keyed); Kononova, 1995: 81 (keyed); Kononova & Petrov, 2002: 55 (keyed).

Gryon simile Kozlov & Kononova: Johnson, 1992: 396 (cataloged, type information); Kononova & Kozlov, 2008: 326, 378 (description, keyed).

Gryon solutum Kononova

Gryon solutus Kononova, 2001: 1472 (original description); Kononova & Petrov, 2002: 53 (keyed); Fabritius & Popovici, 2007: 15, 21 (description, keyed).

Gryon solutum Kononova: Kononova & Kozlov, 2008: 323, 350 (description, keyed).

Comments. We leave this species in *Gryon* based on the original description, "The head sculpture is fine-grained. The frontal impression is distinct, its sculpture is slightly smoothed."

Gryon sparsum Kozlov & Kononova

Gryon sparsum Kozlov & Kononova, 2004: 207 (original description); Kononova & Kozlov, 2008: 328, 397 (description, keyed); Timokhov, 2019b: 48 (catalog of species of Russia).

Comments. The illustrations in the original description are consistent with placement with *Gryon*. We thus choose to leave it in this genus until direct examination of the holotype can occur.

Gryon spennum Kozlov & Lê

Holotype images in MBD: IEBR 0146

Gryon spennum Kozlov & Lê, 1992: 212, 221 (original description, assigned to *miselum* species group, keyed).
Gryon spennus Kozlov & Lê, 1996: 10 (description); Lê, 2000: 97, 131 (description, keyed, type information).

Gryon striatum (Caleca), comb. nov.

Breviscelio striatus Caleca, 1992: 49, 52 (original description, keyed).

Gryon subfasciatum (Wollaston)

Telenomus subfasciatus Wollaston, 1858: 25 (original description); Kieffer, 1926: 40 (description).
Hadronotus subfasciatus (Wollaston): Dodd, 1920a: 350 (generic transfer).
Gryon subfasciatus (Wollaston): Masner, 1965: 78 (type information, generic transfer); Mineo, 1980a: 201 (description).
Gryon subfasciatum (Wollaston): Graham, 1984: 99 (emendation); Johnson, 1992: 396 (cataloged, type information).

Comments. Neither the original description nor the redescription by Mineo (1980a) enables unambiguous generic placement. We leave this species in *Gryon* until the holotype specimen can be examined.

Gryon szaboi Mineo

Hadronotellus hungaricus Szabó, 1966: 422, 423 (original description, keyed).
Gryon hungaricus (Szabó): Kozlov, 1978: 619 (description, generic transfer); Mineo, 1979a: 250 (variation); Kozlov & Kononova, 1989: 80 (keyed); Kozlov & Kononova, 1990: 268, 292 (description, keyed); Kononova & Petrov, 2002: 55 (keyed); Fabritius & Popovici, 2007: 16 (keyed).
Gryon szaboi Mineo: Mineo, 1991: 11, 12 (replacement name for *Hadronotellus hungaricus* Szabó, description, assigned to *hungaricum* species group, keyed); Mineo & Caleca, 1994: 120 (distribution).

Gryon hungaricum (Szabó): Johnson, 1992: 385 (cataloged, type information); Kozlov & Kononova, 2008: 329, 403 (description, keyed).

Comments. We leave this species in *Gryon* based on Mineo's (1991) assignment of it to the *hungaricum* group.

Gryon szelenyii (Szabó)

Holotype images: https://zenodo.org/record/4521320#.YCGzRnlOlaQ

Pannongryon szelenyii Szabó, 1966: 435 (original description, keyed).
Gryon szelenyii (Szabó): Kozlov, 1971: 48, 49 (diagnosis, generic transfer); Kozlov, 1978: 620 (description); Mineo & Szabó, 1978a: 93 (description); Mineo, 1980a: 196 (description); Kozlov & Kononova, 1989: 79 (keyed); Kozlov & Kononova, 1990: 267, 288 (description, keyed); Johnson, 1992: 397 (cataloged, type information); Kononova & Petrov, 2002: 54 (keyed); Fabritius & Popovici, 2007: 26, 66 (keyed); Kononova & Kozlov, 2008: 326, 375 (description, keyed).
Pannongryon szelenyi Szabó: Mineo, 1991: 38 (misspelling).
Gryon szeleneyi (Szabó): Mineo, 1991: 38 (description, assigned to *myrmecophilum* species group, misspelling).

Gryon tardum Kononova & Fursov

Gryon tardus Kononova & Fursov: Kononova & Fursov, 2005a: 593 (original description); Kononova & Fursov, 2005b: 303 (description).
Gryon tardum Kononova & Fursov: Kononova & Kozlov, 2008: 330, 410 (description, keyed).

Comments. This species remains *Gryon* based on the original description "Frontal depression shallow, smooth, shining, with distinct longitudinal carina, almost reaching the anterior ocellus," and Figure 1–4 which illustrates the presence of facial striae and a somewhat protruding clypeus.

Gryon tauricum Kozlov & Kononova

Gryon tauricus Kozlov & Kononova, 1989: 80, 93 (original description, keyed); Kononova & Petrov, 2002: 55 (keyed).
Gryon tauricum Kozlov & Kononova: Kononova & Kozlov, 2008: 329, 405 (description, keyed); Timokhov, 2019b: 47 (catalog of species of Russia).

Comments. This species remains *Gryon* based on the original description.

***Gryon tiliarum* (Kononova & Petrov) comb. nov.**

Exon tiliarum Kononova & Petrov, 2002: 57 (original description, keyed); Kononova & Kozlov, 2008: 447, 450 (description, keyed, generic transfer).

***Gryon thema* Mineo**

Holotype images: https://zenodo.org/record/4521325#.YCGz93lOlaQ

Gryon thema Mineo, 1991: 38 (original description, assigned to *myrmecophilum* species group); Mineo & Caleca, 1994: 120 (distribution).

***Gryon tobiasi* Kozlov & Kononova**

Holotype images: https://zenodo.org/record/5600422#.YXgarfnMJaQ

Gryon tobiasi Kozlov & Kononova, 2004: 207 (original description); Kononova & Kozlov, 2008: 327, 387 (description, keyed); Timokhov, 2019b: 48 (catalog of species of Russia).

***Gryon triangulum* Masner**

Holotype images in MBD: CNC No. 17018

Gryon triangulum Masner, 1983: 135, 171 (original description, keyed); Sarazin, 1986: 979 (type information); Johnson, 1992: 397 (cataloged, type information).

***Gryon trjapitzini* Kozlov & Kononova**

Gryon trjapitzini Kozlov & Kononova, 1989: 79, 90 (original description, keyed); Kozlov & Kononova, 1990: 267, 283 (description, keyed); Johnson, 1992: 397 (cataloged, type information); Kononova, 1995: 81 (keyed); Kononova & Petrov, 2002: 55 (keyed); Fabritius & Popovici, 2007: 29, 68 (keyed); Kononova & Kozlov, 2008: 327, 384 (description, keyed); Timokhov, 2019b: 48 (catalog of species of Russia).

Comments. This species remains in *Gryon* based on characters in the original description, "Frontal depression shallow, smooth, mirror-shiny. The head is fine-grained."

***Gryon turcicum* Kononova & Petrov**

Gryon turcicus Kononova & Petrov, 2001: 1471 (original description); Kononova & Petrov, 2002: 53 (keyed).

Gryon turcicum Kononova & Petrov: Kononova & Kozlov, 2008: 323, 347 (description, keyed).

Comments. The original description of this species is very short and states that the surface sculpture of the head and mesosoma is like that of *Gryon rubrum*.

Gryon ukrainicum (Kozlov & Kononova) comb. nov.

Eremioscelio ukrainica Kozlov & Kononova, 1990: 311, 314 (original description, keyed); Johnson, 1992: 373 (cataloged, type information); Fabritius & Popovici, 2007: 36, 40 (description, keyed).
Eremioscelio ukrainicus Kozlov & Kononova: Kononova & Kozlov, 2008: 452, 453 (description, keyed); Timokhov, 2019b: 47 (catalog of species of Russia).

Gryon valeria Talamas & Timokhov, nom. n.

Eremioscelio tauricus Kozlov & Kononova, 1990: 311, 317 (original description, keyed); Johnson, 1992: 373 (cataloged, type information); Fabritius & Popovici, 2007: 36, 38 (description, keyed); Kononova & Kozlov, 2008: 452, 457 (description, keyed, generic transfer); Timokhov, 2019b: 47 (catalog of species of Russia).

Comments. We transfer this species to *Gryon* based on its prior placement in *Eremioscelio*, which results in homonymy with *Gryon tauricum* Kozlov & Kononova (1989). We here provide a euphonic replacement name, "valeria", to be treated as a noun in apposition.

Gryon verum Kozlov & Kononova

Gryon verus Kozlov & Kononova, 1989: 79, 91 (original description, keyed); Kozlov & Kononova, 1990: 267, 284 (description, keyed); Kononova & Petrov, 2002: 54 (keyed).
Gryon verum Kozlov & Kononova: Johnson, 1992: 398 (cataloged, type information); Kononova & Kozlov, 2008: 326, 372 (description, keyed).

Comments. The description from Kozlov & Kononova (1990) stated, "The frontal impression above the antenna is deep, the granularity of the impression is well pronounced." No mention of transverse striae supports leaving this species in *Gryon*, but examination of the holotype is needed for confident placement.

Gryon xanthogaster (Ashmead)

Figures 83–87; Holotype images in MBD: USNMENT00989056

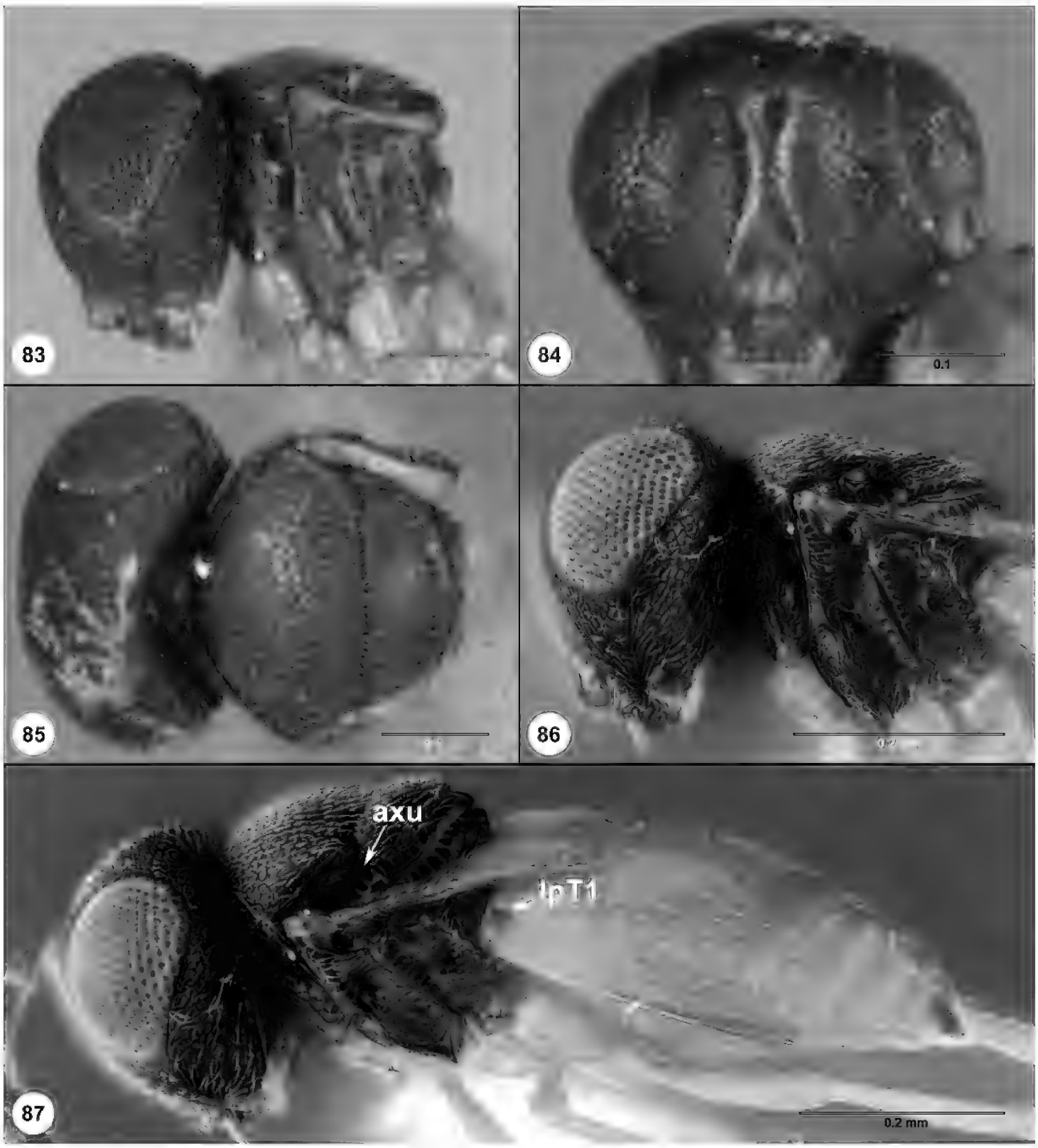
Acolus xanthogaster Ashmead, 1893: 174 (original description).
Psilacolus xanthogaster (Ashmead): Kieffer, 1910: 101 (generic transfer); Kieffer, 1926: 152, 153 (description, keyed).
Acoloides xanthogaster (Ashmead): Muesebeck & Walkley, 1951: 696 (generic transfer).
Gryon xanthogaster (Ashmead): Muesebeck & Masner, 1967: 299 (generic transfer); Masner & Muesebeck, 1968: 37 (type information); Masner, 1983: 133, 163 (description, keyed); Johnson, 1992: 398 (cataloged, type information).

Comments. Masner (1983) described *G. xanthogaster* as having transverse ridges in the frontal depression and tridentate mandibles, characters that would place this species in *Hadronotus*. However, the holotype specimen does not have transverse ridges in the frontal depression (Figure 84). We identified specimens as *G. xanthogaster* based on their congruence with the morphology of the head and mesosoma of the holotype (Figures 83–85) and the yellow metasoma, as is referenced by the name of this species. An example of a recently collected specimen of *G. xanthogaster* is illustrated in Figures 86–87), which shows the striate axillula and lateral pit on T1.

We suspect that the concept of *G. xanthogaster* from Masner (1983) applies to *Hadronotus bicolor* (Figures 88–91), a species of similar size and color pattern that was originally described from the Caribbean. As was mentioned by Masner (1983), this species is somewhat common in Florida, although we have recorded specimens from Washington, DC.

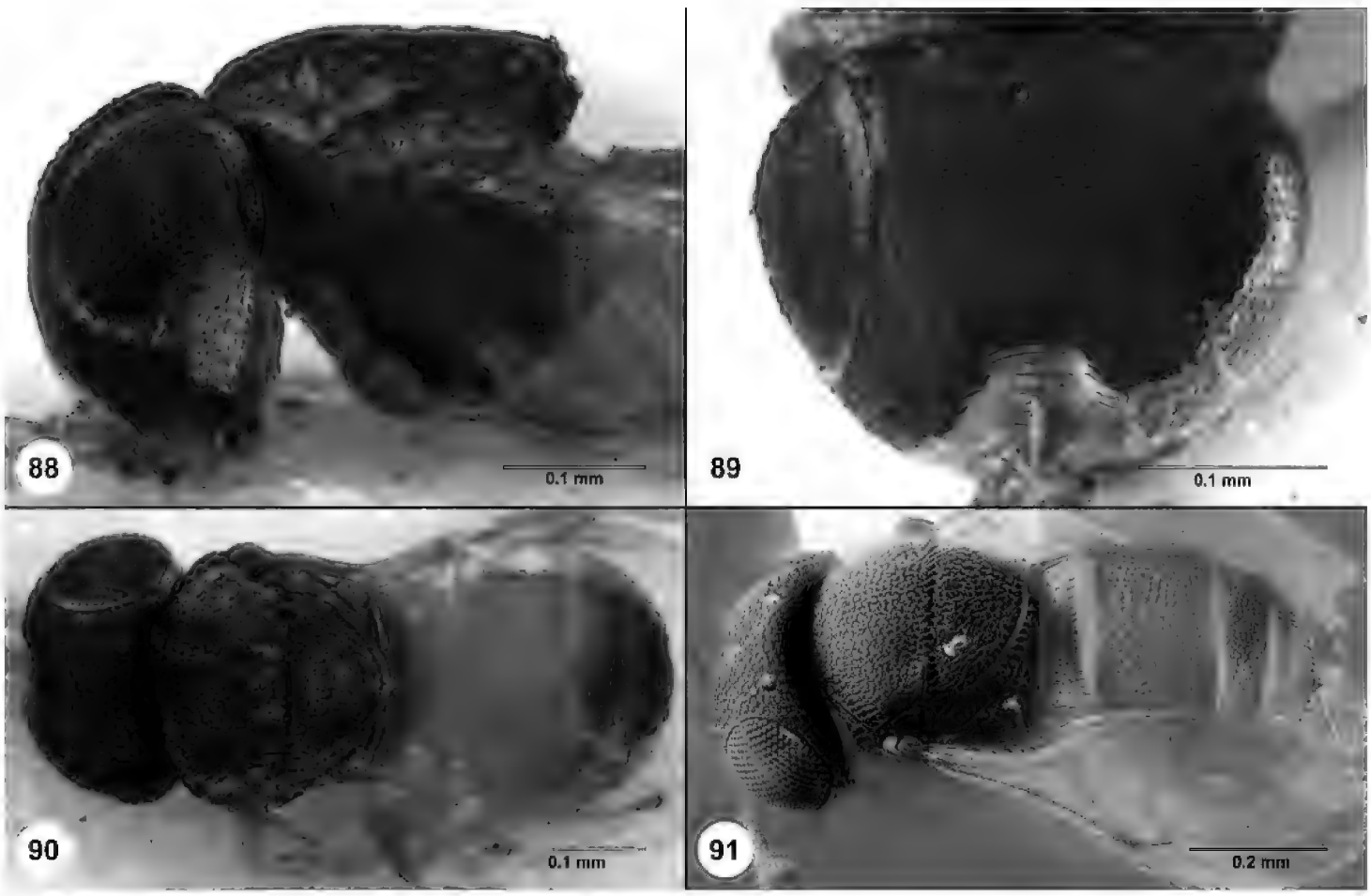
Hadronotus Förster

Hadronotus Förster, 1856 **stat. rev.**: 101, 105 (original description. Type: *Hadronotus exsculptus* Förster, first included species, keyed. Synonymized by Nixon (1936), Masner (1961)); Walker, 1874: 10 (keyed); Howard, 1886: 172 (keyed); Cresson, 1887: 248, 314 (catalog of species of U.S. and Canada); Cresson, 1887: 84 (keyed); Ashmead, 1893: 210, 211, 229 (description, keyed, key to species of U.S. and Canada); Ashmead, 1894: 217, 229 (key to species of St. Vincent, keyed); Ashmead, 1896: 265 (keyed); Dalla Torre, 1898: 498 (catalog of species); Ashmead, 1900: 328 (list of species of West Indies); Ashmead, 1903: 92, 94 (keyed); Kieffer, 1908: 119 (keyed); Brues, 1908: 27, 28, 37, 51 (diagnosis, list of species, keyed); Kieffer, 1910: 65, 81 (description, list of species, keyed); Brues, 1910: 47 (key to species of North America); Kieffer, 1912: 56 (key to species of Seychelles); Dodd, 1913a: 131 (keyed); Kieffer, 1913: 230, 235 (description, key to species of Europe and Algeria); Dodd, 1915: 18 (key to species of Australia, Java, and Fiji); Brues, 1916: 543, 544 (keyed); Kieffer, 1926: 271, 453 (description, keyed, key to species); Nixon, 1934: 1 (description, key to new species described); Nixon, 1934: 290 (description, key to species of Africa); Jansson, 1939: 172 (keyed); Maneval, 1940: 112, 113 (keyed); Mani, 1941: 20, 26 (catalog of species of India, keyed); Risbec, 1950: 585, 591 (key



Figures 83–87. *Gryon xanthogaster* **83** holotype female (USNMENT00989056), head and mesosoma, lateral view **84** holotype female (USNMENT00989056), head, anterior view **85** holotype female (USNMENT00989056), head and mesosoma, dorsal view **86** female (UCFC 026 738), head and mesosoma lateral view **87** female (UCFC 026 738), habitus, dorsolateral view.

to species of Ethiopian region, keyed); Muesebeck & Walkley, 1951: 704 (catalog of species of U.S. and Canada); Muesebeck & Walkley, 1956: 357 (citation of type species); Masner, 1958: 42 (status of subgenera, delimitation of species groups); Masner, 1961: 158 (junior synonym of *Gryon* Haliday); Szabó, 1966: 421, 429 (description, key to Palearctic species known to the author, keyed); Baltazar, 1966: 182 (cataloged, catalog of species of the Philippines); Hellén, 1971: 5, 22 (description, keyed); Carpenter, 1992: 471 (fossil references).



Figures 88–91. *Hadronotus bicolor* **88** holotype female (USNMENT01109345), head and mesosoma, lateral view **89** holotype female (USNMENT01109345), head, anterodorsal view **90** holotype female (USNMENT01109345), habitus, dorsal view **91** female (FSCA 00091193), dorsolateral view.

Comments. The holotype specimen of *Hadronotus exsculptus* is missing its head (Figures 92–94), but the morphology of the mesosoma and metasoma clearly match the generic concept that we associate with Clade B: T1 without lateral pit (Figure 93), hind tibia without subgenual spines (Figure 94), metapleuron setose (Figure 94). The nearly parallel arrangement of the acetabular carina and mesopleural carina, and transverse shape of foveae in the prespecular sulcus are characters known to us from other species of *Hadronotus* and will be useful for treating *H. exsculptus* at the species level in future studies.

Muscidea Motschoulsky, 1863 **syn. n.**: 70 (original description. Type: *Muscidea pubescens* Motschoulsky, by monotypy. Synonymized by Masner (1976)); Ashmead, 1904a: 326 (keyed); Masner, 1976: 57 (junior synonym of *Gryon* Haliday).

Hadronotoides Dodd, 1913b **syn. n.**: 171 (original description. Type: *Hadronotus pentatomus* Dodd, by monotypy and original designation. Treated as junior synonym of *Gryon* by Caleca (1990)); Kieffer, 1926: 266, 474 (description, keyed, key to species); Brues, 1940: 81 (description); Mani, 1941: 19, 27 (catalog of species of India, keyed); Muesebeck & Walkley, 1956: 357 (citation of type species); Masner, 1976: 7, 59 (description, keyed); Mani & Sharma, 1982: 151 (keyed); Mineo & Villa, 1982b: 175 (taxonomic value of pleural structures, clypeus, and antennal sensilla); Mineo & Villa, 1982a: 139 (taxonomic value of structures on the posterior surface of the head); Galloway & Austin, 1984: 6, 81 (diagnosis, list of species

described from Australia, keyed); Johnson, 1992: 398 (cataloged, catalog of world species); Carpenter, 1992: 471 (fossil references).

Platyteleia Dodd, 1913a **syn. n.**: 131, 153 (original description. Type: *Platyteleia latipennis* Dodd, by monotypy and original designation); Dodd, 1914b: 79 (description); Kieffer, 1926: 269, 408 (description, keyed, key to species); Muesebeck & Walkley, 1956: 386 (citation of type species); Masner, 1958: 42 (status of subgenera, delimitation of species groups); Masner, 1961: 158 (junior synonym of *Gryon* Haliday); Szabó, 1966: 421, 429 (description, key to Palearctic species known to the author, keyed); Baltazar, 1966: 182 (cataloged, catalog of species of the Philippines); Hellén, 1971: 5, 22 (description, keyed); Galloway & Austin, 1984: 78 (junior synonym of *Gryon* Haliday); Carpenter, 1992: 471 (fossil references).

Telenomoides Dodd, 1913a **syn. n.** : 158, 168 (original description. Type: *Telenomoides flavipes* Dodd, by original designation. Key to species of Australia, keyed); Muesebeck & Walkley, 1956: 402 (citation of type species).

Comments. Mineo (1990a) treated *Telenomoides flavipes* as a junior synonym of *Gryon orestes* (Dodd), implicitly making *Telenomoides* a junior synonym of *Gryon*. Examination of the holotype specimen leads us to treat *Telenomoides* as a junior synonym of *Hadronotus* based on the presence of five clavomeres, the shape of the clypeus, and the form of foveae along anterior T1.

Notilena Brèthes, 1913 **syn. n.**: 84 (original description. Type: *Notilena Gallardoi* Brèthes, by monotypy and original designation); Muesebeck & Walkley, 1956: 375 (citation of type species); De Santis & Esquivel, 1966: 96 (junior synonym of *Gryon* Haliday).

Comments. We remove *Notilena* from *Gryon* and treat it as a synonym of *Hadronotus* based on characters in the original description, "Capite punctato-umbilicato, facie longitrorsum impressa, utrinque transverse striata et in medio antennas versus longitrorsum cristata," which we interpret to indicate that the sculpture of the head is punctate-umbilicate and that the antennal scrobe has transverse striation.

Austroscelio Dodd, 1914c **syn. n.**: 93 (original description. Type: *Sparasion nigricoxa* Dodd, by original designation. Synonymized by Galloway, in Galloway & Austin (1984)); Kieffer, 1926: 266, 473 (description, keyed, key to species); Muesebeck & Walkley, 1956: 334 (citation of type species); Galloway & Austin, 1984: 78 (junior synonym of *Gryon* Haliday).

Hadrophanurus Kieffer, 1926 **syn. n.**: 15, 130 (original description. Type: *Telenomus pennsylvanicus* Ashmead, by monotypy, keyed. Synonymized by Masner (1961)); Muesebeck & Walkley, 1951: 694 (catalog of species of U.S. and Canada); Muesebeck & Walkley, 1956: 357 (citation of type species); Masner, 1961: 158 (junior synonym of *Gryon* Haliday); Subba Rao & Chacko, 1962: 479 (key to species).

Diagnosis. Sculpture of head and mesosoma highly variable, ranging from coriaceous microsculpture to coarsely areolate or rugose; mandibular dentition variable, teeth of unequal size; clypeus not projecting; ventral frons without facial striae; antennal scrobe with macrosculpture ranging from transversely striate to areolate rugose; anten-

Figures 92–94. *Hadronotus exsculptus*, holotype female (NHMW-HYM #0002996), mesosoma and metasoma **92** posterodorsal view **93** dorsal view **94** lateral view.

nal scrobe often delimited by carinae; female antenna with 10 flagellomeres, four to seven clavomeres; sculpture of mesoscutum and mesoscutellum variable, ranging from coriaceous microsculpture to coarsely areolate, striate or rugose; epomial carina variable, sometimes extending dorsally to pronotal shoulder; netrion absent; mesoscutal humeral sulcus and mesoscutal suprahumeral sulcus variable: absent or indicated by a furrow or line of foveae; mesoscutum with or without humeral pit; sculpture of axillula variable, sometimes with parallel carina between coarse foveae, but not distinctly striate; metapleuron divided dorsoventrally by a change in sculpture or setation; hind tibia without subgenual spines; foveae along anterior T1 decreasing in size laterally, not bordered laterally by a carina or pit.

Comments. *Hadronotus* is morphologically variable and to our knowledge is not united by any single character.

Species of *Hadronotus*

***Hadronotus achille* (Mineo), comb. nov.**
Holotype images: https://zenodo.org/record/4498931#.YBr9QnlOlaQ

Gryon achille Mineo, 1992: 25 (original description).

***Hadronotus aculeator* (Masner), comb. nov.**
Holotype images in MBD: USNMENT01059225

Gryon aculeator Masner, 1983: 157 (original description); Johnson, 1992: 378 (cataloged, type information).

***Hadronotus aculus* (Mineo), comb. nov.**
Holotype images: https://zenodo.org/record/4498957#.YBsBDHlOlaQ

Gryon aculum Mineo, 1991: 2 (original description, assigned to *aculum* species group).

***Hadronotus acuteangulatus* (Mineo), comb. nov.**
Paratype images: https://zenodo.org/record/4924891#.YMJ6knpKhaQ

Gryon acuteangulatum Mineo, 1991: 3 (original description, assigned to *acuteangulatum* species group).

Comments. We transfer this species based the paratype specimen that we examined as well as characters and Figures 1a–b from the original description, "clava of six antennomeres... the sculpture of the head consists of irregular polygons."

***Hadronotus acutiventris* (Masner), comb. nov.**
Holotype images in MBD: CNC No. 17015

Gryon acutiventre Masner, 1983: 134, 158 (original description, keyed); Johnson, 1992: 378 (cataloged, type information).

***Hadronotus agamennone* (Mineo), comb. nov.**
Paratype images: https://zenodo.org/record/4924896#.YMJ6vnpKhaQ

Gryon agamennone Mineo, 1992: 26 (original description)

Comments. We transfer this species based on a paratype specimen and the original description, "...frontal depression that is striated for not more than

⅔, the remaining being smooth and shiny," and because it was considered by Mineo 1992 to be part of the *oculatum* species group.

***Hadronotus agilis* Ashmead, comb. rev.**

Hadronotus agilis Ashmead, 1896: 799 (original description); Ashmead, 1900: 328 (distribution); Kieffer, 1926: 454, 466 (description, keyed).

Gryon agilis (Ashmead): Masner, 1965: 74 (type information, generic transfer); Masner, 1976: 58 (description).

Gryon agile (Ashmead): Johnson, 1992: 378 (cataloged, type information).

Comments. We transfer this species back to *Hadronotus* based on the original description of the sculpture as "coarsely rugose."

***Hadronotus alames* (Kozlov & Lê), comb. nov.**

Holotype images in MBD: IEBR 0160

Gryon alames Kozlov & Lê, 1992: 233, 237 (original description, assigned to *muscaeforme* species group, keyed); Kozlov & Lê, 1996: 12 (description); Lê, 2000: 100 (description, keyed, type information).

***Hadronotus allanidoddi* (Mineo), comb. nov.**

Holotype images: https://zenodo.org/record/4498975#.YBsFBnlOlaQ

Plastogryon flavipes Dodd, 1914a: 125 (original description. Preoccupied by *Telenomoides flavipes* Dodd (1913a)); Dodd, 1915: 25 (keyed).

Plastogryon (*Heterogryon*) *flavipes* Dodd: Kieffer, 1926: 446, 451 (description, subgeneric assignment, keyed).

Gryon flavipes (Dodd): Galloway, 1976: 91 (type information, generic transfer); Johnson, 1992: 383 (cataloged, type information).

Gryon allanidoddi Mineo: Mineo, 1990b: 55 (replacement name for *Plastogryon flavipes* Dodd, description).

***Hadronotus ambericus* (Peter & Rajmohana), comb. nov.**

Gryon ambericum Peter & Rajmohana, 2014: 6711 (original description, diagnosis, placed in *leptocorisae* species group).

Comments. Our transfer of this species to *Hadronotus* is based on images provided in the original description.

***Hadronotus amerares* (Kozlov & Lê), comb. nov.**
Holotype images in MBD: IEBR 0161

Gryon amerares Kozlov & Lê, 1992: 230, 237 (original description, assigned to *muscaeforme* species group, keyed).
Gryon ameraris Kozlov & Lê, 1996: 11 (description); Lê, 2000: 99, 101 (description, keyed, type information).

***Hadronotus americanus* (Mineo), comb. nov.**

Gryon americanum Mineo, Mineo & Caleca,1994: 130 (original description)

Comments. We transfer this species based on the original description, "frontal depression deep and large, crossed by dense and parallel transverse striae."

***Hadronotus amissus* (Kozlov & Kononova), comb. nov.**

Gryon amissus Kozlov & Kononova, 1989: 87 (original description, keyed); Kozlov & Kononova, 1989: 266, 276 (description, keyed).
Gryon amissum Kozlov & Kononova: Kononova & Kozlov, 2008: 324, 351 (description, keyed); Timokhov, 2019b: 47 (catalog of species of Russia).

Comments. We transfer this species based on the original description, "Frontal depression above antennae well pronounced, transversely striated."

***Hadronotus amitto* (Kozlov & Kononova), comb. nov.**

Gryon amitto Kozlov & Kononova, 1989: 87 (original description, keyed).

Comments. We transfer this species based on the original description, "Frontal depression above antennae well pronounced, transversely striated."

***Hadronotus anasae* (Ashmead), comb. rev.**
Holotype images in MBD: USNMENT00979994

Telenomus anasae Ashmead, 1887: 23 (original description).
Hadronotus rugosus Howard, 1889: 242 (original description. Synonymized by Masner (1983)); Ashmead, 1893: 230, 232 (description, keyed); Brues, 1910: 47 (keyed);

Kieffer, 1926: 454, 463 (description, keyed); Masner, 1983: 139 (junior synonym of *Gryon anasae* (Ashmead)); Johnson, 1992: 378 (type information).

Hadronotus anasae (Ashmead): Ashmead, 1893: 231, 233 (generic transfer, description, keyed); Brues, 1910: 47 (keyed); Brues, 1916: 555 (description); Kieffer, 1926: 454, 464 (description, keyed).

Gryon anasae (Ashmead): Muesebeck & Masner, 1967: 299 (generic transfer); Masner & Muesebeck, 1968: 34 (lectotype designation); Masner, 1983: 134, 139 (description, synonymy, keyed); Mineo & Caleca, 1987a: 32 (description); Johnson, 1992: 378 (cataloged, type information).

Gryon rugosus (Howard): Muesebeck & Masner, 1967: 299 (generic transfer); Masner & Muesebeck, 1968: 36 (lectotype designation).

Gryon rugosum (Howard): Mineo & Caleca, 1987a: 34 (description).

***Hadronotus ancinla* (Kozlov & Lê), comb. nov.**

Holotype images: https://bdj.pensoft.net/article/47687/

Gryon ancinla Kozlov & Lê, 1992: 236, 238 (original description, assigned to *muscaeforme* species group, keyed); Kozlov & Lê, 1996: 11 (description); Lê, 2000: 98, 102 (description, keyed, type information).

Gryon clavaerum Kozlov & Lê, 1992: 233, 237 (original description, assigned to *muscaeforme* species group, keyed).

Gryon clavaerus Kozlov & Lê, 1996: 12 (description); Lê, 2000: 99, 108 (description, keyed, type information); Chen et al., 2020: 12 (junior synonym of *Gryon ancinla* Kozlov & Lê)

***Hadronotus anserculus* (Mineo), comb. nov.**

Figure 13; Holotype images: https://zenodo.org/record/4499013#.YBsHqHlOlaQ

Gryon anserculum Mineo, 1991: 7 (original description, assigned to *aureum* species group).

***Hadronotus apex* (Kozlov & Kononova), comb. nov.**

Paratype images: https://zenodo.org/record/5603602#.YXlaE_nMJaQ

Gryon apex Kozlov & Kononova, 2004: 195 (original description); Kononova & Kozlov, 2008: 324, 358 (description, keyed).

***Hadronotus argus* (Kononova), comb. nov.**

Gryon argus Kononova, 2005: 1353 (original description)

Comments. From the original description, "The frontal indentation is superficial, not bordered by an arcuate keel, in transverse wrinkles, with a distinct longitudinal keel." The summary of the original publication, written in English, states that "*Gryon argus* is similar to *G. coronatum*, Kononova, but differs in abdomen proportions." Illustrations in the original description of *G. coronotum* depict a frontal depression that enables us to place that species in *Hadronotus*. It is on this basis and the presence of "transverse wrinkles" in the frontal depression that we make the generic transfer.

***Hadronotus artus* (Kozlov & Kononova), comb. nov.**
Holotype images: https://zenodo.org/record/4531735#.YCQrVnlOlaQ

Gryon artus Kozlov & Kononova, 1989; 81, 99 (original description); Kozlov & Kononova, 1990: 306 (description, keyed); Johnson, 1992: 379 (catalogued); Kononova & Kozlov, 2008: 333, 439 (description, keyed).

Comments. *Mirotelenomus artus* Kozlov was transferred to *Exon* by Masner (1980) and to *Gryon* by Mineo (1980a). The description of *Gryon artus* Kozlov & Kononova thereby created a homonym, one that is resolved by our transfer of this species to *Hadronotus*.

***Hadronotus atrocoxalis* Ashmead, comb. rev.**

Hadronotus atrocoxalis Ashmead, 1896: 799 (original description); Ashmead, 1900: 328 (distribution); Kieffer, 1926: 455, 466 (description, keyed).
Gryon atrocoxalis (Ashmead): Masner, 1965: 74 (type information); Masner, 1976: 58 (description, systematic position); Masner, 1979: 792, 794 (description, keyed).
Gryon atrocoxale (Ashmead): Johnson, 1992: 379 (cataloged, type information).

Comments. The original description indicates that this species is rugose, and separately states "Abdomen rugose", leading us to believe that the former refers to the head or mesosoma. Masner (1976) commented that it "runs to *floridanus*-Ashmead group yet of much finer sculpture" and Masner (1979) placed this species in the *variicornis* species group, which we consider to belong in *Hadronotus*.

***Hadronotus ater* (Masner), comb. nov.**
Figure 11: Holotype images in MBD: CNC No. 17012

Gryon atrum Masner, 1983: 135, 139 (original description, keyed); Sarazin, 1986: 972 (type information); Johnson, 1992: 379 (cataloged, type information).

***Hadronotus aureus* (Dodd), comb. nov.**

Plastogryon aureus Dodd, 1914f: 256 (original description); Dodd, 1915: 24 (keyed).
Plastogryon (*Heterogryon*) *aureus* Dodd: Kieffer, 1926: 447, 450 (description, subgeneric assignment, keyed).
Gryon aureus (Dodd): Galloway, 1976: 91 (type information, generic transfer).
Gryon aureum (Dodd): Mineo, 1991: 7 (assigned to *aureum* species group); Johnson, 1992: 379 (cataloged, type information).

Comments. The original description is insufficient to determine if this species belongs in *Gryon* or *Hadronotus*. Mineo (1991) assigned *Gryon aureum* to an eponymous species group but without explicitly stating if the holotype specimen of *Plastogryon aureus* was examined. The characters in the description of the *aureum* species group indicate that it belongs in *Hadronotus* and it is on this basis that we transfer it.

***Hadronotus austini* (Mineo), comb. nov.**
Paratype images: https://zenodo.org/record/4924904#.YMJ6wHpKhaQ

Gryon austini Mineo, 1991: 6 (original description, assigned to *acuteangulatum* species group).

Comments. The transfer to *Hadronotus* is based on examination of a paratype specimen and characters in the original description: mandibles tridentate, striae present above the frontal depression, and frons sculptured with irregular polygons.

***Hadronotus australicus* (Mineo), comb. nov.**
Holotype images: https://zenodo.org/record/4723897#.YIhY__lKhaQ

Sparasion nigricoxa Dodd, 1914a: 123 (original description. Preoccupied by *Gryon nigricoxa* (Dodd) (1913a)).
Austroscelio nigricoxa (Dodd): Dodd, 1914c: 93 (description, generic transfer, synonymy); Kieffer, 1926: 473 (description, keyed); Galloway, 1976: 85 (type information).
Sparaison australicum Dodd, 1914f: 255 (original description, spelling error. Synonymized by Dodd (1914c)); Johnson, 1992: 391 (type information).
Sparasion australicum Dodd: Dodd, 1914c: 93 (junior synonym of *Austroscelio nigricoxa* (Dodd)).
Sparasion australicus Dodd: Kieffer, 1926: 299 (description, emendation).
Austroscelio australicum (Dodd): Galloway, 1976: 85 (type information).
Gryon nigricoxa (Dodd): Galloway & Austin, 1984: 80 (generic transfer); Johnson, 1992: 391 (cataloged, type information).

Gryon australicum Mineo: Mineo, 1990b: 52 (replacement name for *Sparasion nigricoxa* Dodd, assigned to *insulare* species group, type information).

***Hadronotus avanus* (Kozlov & Lê), comb. nov.**
Paratype Images in MBD: USNMENT01223638

Gryon avanum Kozlov & Lê, 1992: 231, 237 (original description, assigned to *muscaeforme* species group, keyed).
Gryon avanus Kozlov & Lê, 1996: 12 (description); Lê, 2000: 99, 103 (description, keyed, type information).

***Hadronotus baeiformis* (Marshall), comb. rev.**

Prosacantha baeiformis Marshall, 1892: 75 (original description).
Hoplogryon (*Hoplogryon*) *baeiformis* (Marshall): Kieffer, 1910: 96 (generic transfer, subgeneric assignment).
Hadronotus baeiformis (Marshall): Kieffer, 1926: 455, 468 (generic transfer, description, keyed).
Gryon baeiforme (Marshall): Johnson, 1992: 379 (cataloged).

Comments. The original description states that the head is "partout fortement ponctuée" which translates to "strongly punctuated everywhere" and is the basis for transferring this species to *Hadronotus*.

***Hadronotus barbiellinii* Costa Lima, comb. rev.**
Hadronotus Barbiellinii Costa Lima, 1940: 65 (original description).
Gryon barbiellinii (Costa Lima): De Santis, 1980: 312 (generic transfer); Johnson, 1992: 379 (cataloged, type information).

Comments. This species is returned to *Hadronotus* based on characters in the original description, "Face (frontal space located above the base of the antennae and inside the curved protruding line that separates it from the forehead) presenting, in the middle, deep longitudinal groove, transversely striated, at the sides of which there is an oblique series of 4 to 5 relatively wide areolas, immediately into the small areolas that border the edge of the eye and out of another series of areolas, much smaller, which are parallel to it."

***Hadronotus basokoi* Risbec, comb. rev.**

Hadronotus basokoi Risbec, 1958: 115 (original description).

Gryon basokoi (Risbec): Masner, 1976: 58 (generic transfer, systematic position); Johnson, 1992: 379 (cataloged, type information).

Comments. From the original description, "Quite deep postantennal depressions, clearly limited by two ridges which meet at a sharp angle. Crossed by fairly strong streaks."

***Hadronotus bicolor* Ashmead, comb. rev.**
Figures 88–91; Holotype images in MBD: USNMENT01109345

Hadronotus bicolor Ashmead, 1894: 229, 231 (original description, keyed); Ashmead, 1900: 328 (distribution); Kieffer, 1926: 455, 468 (description, keyed).
Gryon bicolor (Ashmead): Masner, 1976: 58 (generic transfer, taxonomic status); Mineo, 1980a: 190 (removed from synonymy with *Gryon misellum* Haliday); Johnson, 1992: 379 (cataloged).

***Hadronotus bimaculatus* (Mineo), comb. nov.**
Holotype images: https://zenodo.org/record/4499037#.YBsNC3lOlaQ

Gryon bimaculatum Mineo, 1983c: 546, 551 (original description); Johnson, 1992: 380 (cataloged, type information).

***Hadronotus bini* (Mineo), comb. nov.**
Holotype images: https://zenodo.org/record/4499039#.YBsOi3lOlaQ

Gryon bini Mineo, 1983c: 528, 546 (original description); Johnson, 1992: 380 (cataloged).

***Hadronotus blaches* (Kozlov & Lê), comb. nov.**
Holotype images in MBD: IEBR 0048

Gryon blaches Kozlov & Lê, 1992: 225, 227 (original description, assigned to *insulare* species group, keyed).
Gryon blachis Kozlov & Lê, 1996: 10 (description); Lê, 2000: 98, 104 (description, keyed, type information).

***Hadronotus bolivari* Giard, comb. rev.**

Hadronotus Bolivari Giard, 1895: 78 (original description. Type lost from MNHN); Kieffer, 1913: 244 (description).

Hadronotus Proximus Kieffer, 1913: 244 (original description); Johnson, 1992: 380 (type information).
Hadronotus bolivari Giard: Kieffer, 1926: 454, 458 (description, keyed); Szabó, 1966: 430, 433 (description, keyed).
Hadronotus proximus Kieffer: Kieffer, 1926: 454, 459 (description, keyed); Bin, 1974: 455 (type misssing from MCSN); Mineo, 1979a: 237 (lectotype designation).
Hadronotus ochraceus Szabó, 1966: 429, 431 (original description); Mineo, 1979a: 237 (junior synonym of *Hadronotus Bolivari* Giard); Johnson, 1992: 380 (type information).
Gryon proximus (Kieffer): Kozlov, 1978: 620 (description); Kozlov & Kononova, 1989: 79 (keyed); Kozlov & Kononova, 1990: 267, 280 (description, keyed); Kononova & Petrov, 2002: 54 (keyed).
Gryon bolivari (Giard): Mineo, 1979: 237 (description, generic transfer); Mineo, 1981: 119, 120 (description, type information, keyed); Johnson, 1992: 380 (cataloged, type information); Mineo & Caleca, 1994: 117 (distribution, assigned to *muscaeforme* subgroup of *muscaeforme* group); Kononova & Kozlov, 2008: 325, 362 (description, keyed); Timokhov, 2019b: 47 (catalog of species of Russia).

Comments. We return this species to *Hadronotus* based on a character in the original description, "head black, punctate."

***Hadronotus bosellii* (Mineo & Szabó), comb. nov.**
Holotype images: https://zenodo.org/record/4499042#.YBsQeXlOlaQ

Gryon bosellii Mineo & Szabó, 1978b: 113 (original description); Mineo, 1981a: 119, 124 (diagnosis, keyed); Johnson, 1992: 380 (cataloged, type information); Mineo & Caleca, 1994: 117 (distribution, assigned to muscaeforme subgroup of *muscaeforme* group); Kononova & Petrov, 2002: 54 (keyed); Kononova & Kozlov, 2008: 325, 367 (description, keyed).

***Hadronotus brasiliensis* Costa Lima, comb. rev.**

Hadronotus brasiliensis Costa Lima, 1928: 1 (original description).
Gryon brasiliensis (Costa Lima): De Santis, 1980: 312 (generic transfer).
Gryon brasiliense (Costa Lima): Johnson, 1992: 380 (cataloged, type information).

Comments. We transfer this species back to *Hadronotus* based on characters in the original description, "antennal suture or pit distinctly separated from the forehead by an arched cross-striated trench, leading the most saline striae of the midline to the areolas of the face."

***Hadronotus cabrucae* (Mineo), comb. nov.**
Holotype images: https://zenodo.org/record/4499046#.YBsRxXlOlaQ

Gryon cabrucae Mineo, Mineo & Caleca, 1994: 126 (original description, assigned to *floridanum* group).

***Hadronotus canus* (Mineo), comb. nov.**
Figure 14; Holotype images: https://zenodo.org/record/4499060#.YBsUrnlOlaQ

Gryon canum Mineo, 1991: 15 (original description, assigned to *leptocorisae* species group); Mineo & Caleca, 1994: 122 (distribution).

***Hadronotus carinatifrons* Ashmead, comb. rev.**
Holotype images: https://zenodo.org/record/4499077#.YBscUnlOlaQ

Hadronotus carinatifrons Ashmead, 1894: 229, 230 (original description); Ashmead, 1900: 328 (distribution); Brues, 1910: 47 (keyed); Kieffer, 1926: 455, 467 (description, keyed).
Gryon carinatifrons (Ashmead): Muesebeck & Masner, 1967: 299 (generic transfer); Alayo Dalmau, 1973: 99 (cataloged); Masner, 1983: 134, 143 (type information, spelling error); Mineo & Caleca, 1987a: 32 (description, keyed); Johnson, 1992: 380 (cataloged, type information).
Gryon carinatiforns (Ashmead): Masner, 1976: 58 (type information, spelling error).

***Hadronotus charon* Nixon, comb. rev.**
Holotype images: https://zenodo.org/record/4499096#.YBsb6XlOlaQ

Hadronotus charon Nixon: Nixon, 1934b: 292, 306 (description); Risbec, 1950: 592, 595 (original description).
Gryon charon (Nixon): Masner, 1965: 75 (type information); Mineo, 1982b: 312 (description); Mineo, 1983a: 18 (description, variation, keyed); Johnson, 1992: 380 (cataloged, type information).

***Hadronotus chelinideae* (Masner), comb. nov.**
Holotype images in MBD: USNMENT01059234
Gryon chelinideae Masner, 1983: 133, 159 (original description, keyed); Johnson, 1992: 381 (cataloged, type information).

***Hadronotus chinchillae* (Caleca), comb. nov.**
Holotype images: https://zenodo.org/record/4499104#.YBsfwXlOlaQ

Gryon chinchillae Caleca, 1990a: 119, 120 (original description, keyed).

***Hadronotus circus* (Kozlov & Lê), comb. nov.**
Paratype images in MDB: USNMENT01223669

Gryon circum Kozlov & Lê, 1992: 223, 227 (original description, assigned to *insulare* species group, keyed).
Gryon circus Kozlov & Lê, 1996: 10 (description); Lê, 2000: 97, 107 (description, keyed, type information).

Comments. The frons of this species suggests close relation to *H. watshami*.

***Hadronotus clavigrallae* (Mineo), comb. nov.**
Holotype images: https://zenodo.org/record/4499107#.YBshQHlOlaQ

Gryon clavigrallae Mineo, Mineo & Caleca, 1994: 116 (original description, assigned to *fulviventre* subgroup of *muscaeforme* group).

***Hadronotus compoventris* (Kozlov & Lê), comb. nov.**
Holotype images in MBD: IEBR 0163

Gryon compoventre Kozlov & Lê, 1992: (original description, assigned to *muscaeforme* species group, keyed).
Gryon compoventris Kozlov & Lê, 1996: 11 (description); Lê, 2000: 99, 110 (description, keyed, type information).

***Hadronotus coronatus* (Kononova), comb. nov.**

Gryon coronatum Kononova, 2008: 322, 335 (original description, keyed); Timokhov, 2019b: 47 (catalog of species of Russia).

Comments. In the original description, figure 176 illustrates transverse striation across the frontal depression and a female antenna with five clavomeres.

***Hadronotus cous* Nixon, comb. rev.**

Hadronotus cous Nixon, 1934b: 292, 301 (original description, keyed); Risbec, 1950: 592 (keyed).
Gryon cous (Nixon): Masner, 1965: 75 (type information).

Gryon coum (Nixon): Mineo, 1983c: 528, 546 (description, keyed); Johnson, 1992: 381 (cataloged, type information).

Comments. The original description provides characters that enable us to transfer this species to *Hadronotus*, including "Frons with a deep, well-defined impression which is completely margined."

***Hadronotus chromion* (Kozlov & Lê), comb. nov.**
Holotype images in MBD: IEBR 0175

Gryon chromion Kozlov & Lê, 1992: 232, 237 (original description, assigned to *muscaeforme* species group, keyed).
Gryon cromion Kozlov & Lê, 1996: 12 (description, misspelling); Lê, 2000: 100, 112 (description, keyed, type information).

***Hadronotus cultratus* (Masner), comb. nov.**
Paratype images: https://zenodo.org/record/4959367#.YNnSfklKhaQ

Gryon cultratus Masner, 1979: 794, 799 (original description, keyed); Sarazin, 1986: 974 (type information).
Gryon cultratum Masner: Johnson, 1992: 381 (cataloged, type information).

Comments. This species is transferred to *Hadronotus* based on its placement in the *variicorne* group and characters presented in the original description: "head... with coarse transverse polygons", "scutellum with polygons roughly rounded" and examination of a paratype specimen.

***Hadronotus dasyni* Nixon, comb. rev.**

Hadronotus dasyni Nixon, 1934a: 2 (original description, keyed).
Gryon dasyni (Nixon): Masner, 1965: 75 (type information); Mineo, 1990: 90 (keyed); Johnson, 1992: 381 (cataloged, type information).

Comments. The original description and (Figure 1) in Nixon (1934) list and illustrate a form of the frontal depression that clearly places this species in *Hadronotus*, "Frontal impression completely margined by a sharply defined ridge."

***Hadronotus david* (Masner), comb. nov.**
Holotype images: https://cnc.agr.gc.ca/taxonomy/Specimen.php?id=2952

Gryon david Masner, 1979: 793, 798 (original description, keyed); Sarazin, 1986: 974 (type information); Johnson, 1992: 381 (cataloged, type information).

***Hadronotus dessarti* (Mineo), comb. nov.**
Holotype images: https://zenodo.org/record/4502725#.YBw9tXlOlaQ

Gryon dessarti Mineo, 1991: 38 (original description, assigned to *oculatum* species group).

***Hadronotus diadematis* (Mineo), comb. nov.**
Paratype images: https://zenodo.org/record/4959399#.YNnSTklKhaQ

Gryon diadematis Mineo, 1983a: 18, 19 (original description, keyed); Johnson, 1992: 381 (cataloged, type information).

Comments. We transfer this species to *Hadronotus* based on the description of the "completely enframed frontal depression... connected to the anterior ocellus by a ridge" provided in Mineo (1983a) and examination of a paratype specimen.

***Hadronotus dichromos* (Galloway), comb. nov.**
Holotype images: https://zenodo.org/record/4503990#.YBxeBnlOlaQ

*Plastogryon bicolo*r Dodd, 1913b: 171 (original description. Preoccupied by *Hadronotus bicolor* Ashmead (1894)); Dodd, 1915: 24 (keyed).
Plastogryon (*Heterogryon*) *bicolor* (Dodd): Kieffer, 1926: 447, 451 (description, subgeneric assignment, keyed).
Gryon bicolor (Dodd): Galloway, 1976: 91 (type information, generic transfer).
Gryon dichromos Galloway: Galloway & Austin, 1984: 79 (replacement name); Mineo, 1990a: 186 (description of male); Mineo, 1991: 7 (assigned to *charon* species group); Johnson, 1992: 381 (cataloged, type information).

***Hadronotus discolor* (Mineo & Szabó), comb. nov.**
Holotype images: https://zenodo.org/record/4504025#.YBxe8XlOlaQ

Gryon discolor Mineo & Szabó, 1978c: 94 (original description); Johnson, 1992: 382 (cataloged, type information).

***Hadronotus drunores* (Kozlov & Lê), comb. nov.**
Holotype images in MBD: IEBR 0176

Gryon drunores Kozlov & Lê, 1992: 235 (original description, assigned to *muscaeforme* species group).
Gryon drumores Kozlov & Lê, 1992: 237 (keyed, misspelling).
Gryon drunoris Kozlov & Lê, 1996: 11 (description); Lê, 2000: 98, 113 (description, keyed, type information).

***Hadronotus dubius* (Kozlov & Kononova), comb. nov.**
Holotype images: https://zenodo.org/record/4726076#.YXlbFPnMJaQ
Paratype images: https://zenodo.org/record/5603654#.YXlbpPnMJaQ

Gryon dubium Kozlov & Kononova, 2004: 199 (original description); Kononova & Kozlov, 2008: 322, 333 (description, keyed); Timokhov, 2019a: 19 (distribution); Timokhov, 2019b: 47 (catalog of species of Russia).

***Hadronotus elegans* (Dodd), comb. nov.**

Plastogryon elegans Dodd, 1914c: 94 (original description); Galloway, 1976: 111 (type information, status uncertain).
Plastogryon (*Heterogryon*) *elegans* Dodd: Kieffer, 1926: 447, 451 (description, subgeneric assignment, keyed).
Gryon elegans (Dodd): Mineo, 1990a: 185 (generic transfer, type information); Mineo, 1991: 7 (assigned to *aureum* species group); Johnson, 1992: 382 (cataloged, type information).

Comments. Mineo (1990a) stated that he found and examined the holotype specimen of *Plastogryon elegans* in the South Australia Museum. Mineo (1991) placed this species in the *aureum* species group, which he described as having "mandibles subtridentate" and "frontal depression large but moderately deep, crossed by very fine and dense striae." This forms our basis for transferring this species to *Hadronotus*.

***Hadronotus elongatus* Risbec, comb. rev.**
Lectotype images: https://zenodo.org/record/4504271#.YBxm4nlOlaQ

Hadronotus antestiae var. elongatus Risbec, 1950: 597 (original description); Mineo, 1990b: 50 (lectotype designation, synonymy); Johnson, 1992: 383 (type information).
Gryon antestiae var. elongatus (Risbec): Masner, 1976: 58 (generic transfer, type information).
Gryon risbeci Mineo, 1990b: 50 (original description, assigned to *hiberus* species group, a junior objective synonym of *Hadronotus antestiae var. elongatus* Risbec).

***Hadronotus euclidis* (Mineo), comb. nov.**
Holotype images: https://zenodo.org/record/4504306#.YBxoRXlOlaQ

Gryon euclide Mineo, 1992: 21 (original description).

***Hadronotus eugeniae* (Risbec), comb. nov.**
Holotype images: https://zenodo.org/record/4504356#.YBxpenlOlaQ

Microphanurus eugeniae Risbec, 1953: 326 (original description).
Gryon eugeniae (Risbec): Masner, 1976: 58 (generic transfer, type information); Johnson, 1992: 382 (cataloged, type information).

***Hadronotus eurystenis* (Mineo), comb. nov.**
Paratype images: https://zenodo.org/record/5104412#.YO9CaElKhaR

Gryon eurystene Mineo, 1992: 21 (original description)

Comments. Our transfer of this species to *Hadronotus* is based on the original description, which states that this species is "Closely related to *G. canum*" and examination of a paratype specimen

***Hadronotus exsculptus* Förster, comb. rev.**
Figures 92–94; Holotype images: https://zenodo.org/record/4504407#.YBxrf3lOlaQ

Hadronotus exsculptus Förster, 1861: 41 (original description); Dalla Torre, 1885: 76 (reprint of Förster (1861)); Kieffer, 1908: 145 (French translation of Förster (1861)); Kieffer, 1926: 453, 458 (description, keyed).
Hadronotus Exsculptus Förster: Kieffer, 1913: 238 (description).
Gryon exsculptus (Förster): Kozlov, 1978: 620 (description); Mineo, 1979a: 244 (description); Kozlov & Kononova, 1989: 78 (keyed).
Gryon exsculptum (Förster): Mineo, 1981a: 119, 126 (description of male, diagnosis, keyed); Johnson, 1992: 382 (cataloged, type information); Kononova & Kozlov, 2008: 325, 364 (description, keyed); Timokhov, 2019b: 47 (catalog of species of Russia).
Gryon exculptus (Förster): Kozlov & Kononova, 1990: 266, 272 (description, keyed, error); Kononova, 1995: 81 (keyed); Kononova & Petrov, 2002: 54 (keyed).
Gryon exculptum (Förster): Mineo & Caleca, 1994: 117 (spelling error, distribution, assigned to *muscaeforme* subgroup of *muscaeforme* group).

***Hadronotus fervidus* (Mineo), comb. nov.**
Paratype images: https://zenodo.org/record/5018387#.YNnQwklKhaQ

Gryon fervidum Mineo, 1992: 18 (original description).

Comments. The original description is brief, and characters needed to properly place this species are largely absent. We interpret "from upper margin of the frontal depression and because there is no ridge connecting the latter to anterior ocellus" to refer to a carinate margin of the frontal depression, as is seen in *Hadronotus ancinla* (Chen et al. 2020), and which may be connected to the anterior ocellus by a carina. Mineo (1992) placed *G. fervidum* in the *hiberus* group, but the description of the *hiberus* group by Mineo (1990b) is also brief and insufficient for generic placement. We examined the holotype of *Hadronotus lucmon*, described as *Gryon lucmon* concomitantly with *G. fervidum*, which was also placed in the *hiberus* group and which belongs in *Hadronotus*. Our examination of a paratype specimen also supports placement of this species in *Hadronotus*.

***Hadronotus flavios* (Dodd), comb. nov.**
Holotype images: https://zenodo.org/record/4504474#.YBxtSHlOlaQ

Plastogryon flavios Dodd, 1915: 32 (original description).
Gryon flavios (Dodd): Galloway, 1976: 91 (type information, generic transfer); Mineo, 1991: 7 (assigned to *charon* species group); Johnson, 1992: 382 (cataloged, type information).

***Hadronotus flavipes* Ashmead, comb. rev.**
Holotype images in MBD: USNMENT00989868

Hadronotus flavipes Ashmead, 1905: 399 (original description. Preoccupied by *Gryon flavipes* Ashmead (1893). Synonymized with *Telenomus orestes* Dodd by Mineo (1990a)); Kieffer, 1926: 454, 460 (description, keyed); Baltazar, 1966: 182 (cataloged, type information, distribution); Mineo, 1990a: 178 (junior synonym of *Gryon orestes* (Dodd)); Johnson, 1992: 392 (type information).
Plastogryon fuscus Dodd, 1915: 25, 26 (original description, keyed. Synonymized with *Telenomus orestes* Dodd by Mineo (1990a)); Mineo, 1990a: 178 (junior synonym of *Gryon orestes* (Dodd)); Johnson, 1992: 392 (type information).
Telenomus orestes Dodd, 1913a: 167, 168 (original description, keyed).
Liophanurus orestes (Dodd): Kieffer, 1926: 68, 90 (description, generic transfer, keyed).
Hadronotus leptocorisae Nixon, 1934: 2, 5 (original description, keyed. Preoccupied by *Hadronotus leptocorisae* Howard (1885). Synonymized with *Hadronotus flavipes* Ashmead by Mineo (1979)); Mineo, 1979: 247 (junior synonym of *Hadronotus flavipes* Ashmead); Mineo, 1990: 178 (incorrect placement); Johnson, 1992: 393 (type information).
Gryon nixoni Masner: Masner, 1965: 77 (replacement name for *Hadronotus leptocorisae* Nixon, type information, synonymized with *Hadronotus flavipes* Ashmead by Mineo

(1979)); Mineo, 1979: 247 (junior synonym of *Hadronotus flavipes* Ashmead); Mineo, 1981: 119, 139 (description, keyed); Mineo, 1990: 178 (incorrect placement).
Gryon ferus Masner & Muesebeck: Masner & Muesebeck, 1968: 35 (replacement name for *Hadronotus flavipes* Ashmead. Type information. Synonymized with *Telenomus orestes* Dodd by Mineo (1990a)); Mineo, 1990a: 179 (junior synonym of *Gryon orestes* (Dodd)).
Gryon fuscus (Dodd): Galloway, 1976: 91 (type information, generic transfer).
Gryon orestes (Dodd): Johnson, 1988b: 242 (type information, generic transfer); Mineo, 1990a: 178 (synonymy, variation); Johnson, 1992: 392 (cataloged, type information); Kononova & Kozlov, 2008: 324, 356 (description, keyed).

***Hadronotus floridanus* Ashmead, comb. rev.**
Lectotype images in MBD: USNMENT00989854

Hadronotus floridanus Ashmead, 1887: 118 (original description); Ashmead, 1893: 231, 232 (description, keyed); Brues, 1910: 47 (keyed); Kieffer, 1926: 454, 463 (description, keyed).
Hadronotus robustus Brues, 1907: 156 (original description. Synonymized by Masner (1983)); Brues, 1910: 46, 47 (diagnosis of male, keyed); Kieffer, 1926: 454, 464 (description, keyed); Masner, 1983: 136 (junior synonym of *Gryon floridanum* (Ashmead)); Johnson, 1992: 383 (type information).
Gryon robustus (Brues): Masner, 1965: 299 (type information, generic transfer).
Gryon floridanus (Ashmead): Muesebeck & Masner, 1967: 299 (generic transfer); Masner & Muesebeck, 1968: 35 (lectotype designation).
Gryon floridanum (Ashmead): Masner, 1983: 135, 136 (description, synonymy, emendation, keyed); Mineo & Caleca, 1987: 32 (description); Johnson, 1992: 383 (cataloged, type information).

***Hadronotus fulvicoxus* (Komeda & Mita), comb. nov.**

Gryon fulvicoxa Komeda & Mita, in Komeda, Mita, Hirose & Yamagishi, 2020: 101, 128 (original description, keyed).

Comments. The transfer to *Hadronotus* is based on images and characters in the original description.

***Hadronotus fulviventris* Crawford, comb. rev.**
Holotype images in MBD: USNMENT00989855

Hadronotus fulviventris Crawford, 1912: 2 (original description).
Hadronotus antestiae Dodd, 1920a: 351 (original description. Synonymized by Mineo (1979a)); Nixon, 1934b: 292, 306 (emendation of original description, keyed);

Risbec, 1950: 592 (keyed); Mineo, 1979a: 247 (junior synonym of *Gryon fulviventris* (Crawford)); Johnson, 1992: 383 (type information).

Gryon antestiae (Dodd): Masner, 1965: 74 (lectotype designation).

Gryon fulviventris (Crawford): Masner & Muesebeck, 1968: 35 (type information, generic transfer); Mineo, 1979a: 247 (synonymy); Mineo, 1981a: 119, 128 (diagnosis, keyed); Sharma, 1982: 336 (keyed); Lê, 2000: 98, 115 (description, keyed).

Gryon terraesanctae Mineo & Szabó, 1978b: 116 (original description. Synonymized by Mineo (1979a)); Mineo, 1979a: 247 (junior synonym of *Gryon fulviventris* (Crawford)); Johnson, 1992: 383 (type information).

Gryon tico Mineo & Szabó, 1978c: 96 (original description. Synonymized by Mineo (1990a)); Mineo, 1990a: 174 (junior synonym of *Gryon fulviventre* (Crawford)); Johnson, 1992: 383 (type information).

Gryon fulviventre (Crawford): Mineo, 1990a: 174 (emendation, variation); Johnson, 1992: 383 (cataloged, type information); Kononova & Kozlov, 2008: 322, 343 (description, keyed); Rajmohana, 2014: 34 (description, distribution).

***Hadronotus gallardoi* (Brèthes), comb. nov.**

Notilena Gallardoi Brèthes, 1913: 85 (original description).

Gryon gallardoi (Brèthes): De Santis & Esquivel, 1966: 50 (generic transfer); Loiácono, 1980: 173 (description); Mineo & Caleca, 1987a: 37 (description); Johnson, 1992: 383 (cataloged, type information).

Comments. We transfer this species to *Hadronotus* based on characters in the original description, "Head punctate-umbilicate, face longitudinally impressed, crested on both sides, transverse striae and in the midst of the antennae longitudinally crested."

***Hadronotus geminus* (Mineo), comb. nov.**

Gryon geminum Mineo, 1991: 6 (original description, assigned to *acuteangulatum* species group).

Comments. The original description of *G. geminum* is so sparse that it can hardly be considered a description. It merely states that this species differs from *G. austini* by the sculpture of the frons, but with no mention of how it is different. This approach to species descriptions is of no benefit and has created significant obstacles for advancing taxonomy in this group.

***Hadronotus giganteus* (Mineo), comb. nov.**

Holotype images: https://zenodo.org/record/4504654#.YBxzznlOlaQ

Gryon giganteum Mineo, 1983c: 529, 546 (original description, keyed); Johnson, 1992: 384 (cataloged, type information).

***Hadronotus gnidus* Nixon, comb. rev.**
Paratype images: https://zenodo.org/record/4730565#.YIwZxLVKhaQ

Hadronotus gnidus Nixon, 1934b: 292, 305 (original description, keyed. Synonymized by Mineo (1990a)); Risbec, 1950: 592, 595 (variation, keyed); Mineo, 1990a: 174 (junior synonym of *Gryon fulviventre* (Crawford)).
Gryon gnidum (Nixon): Mineo & Caleca, 1994: 117 (treated as valid species, distribution, assigned to *fulviventre* subgroup of *muscaeforme* group).

Comments. The original description compares this species to *H. antestiae* (junior synonym of *H. fulviventris*), and we confirm that *H. fulviventris* belongs in *Hadronotus* based on examination of the holotype. We also examined two paratypes of *H. gnidus*, one male and one female.

***Hadronotus goliath* (Masner), comb. nov.**
Holotype images: https://cnc.agr.gc.ca/taxonomy/Specimen.php?id=2953

Gryon goliath Masner, 1979: 793, 798 (original description, keyed); Sarazin, 1986: 974 (type information); Johnson, 1992: 384 (cataloged, type information).

***Hadronotus grenadensis* Ashmead, comb. rev.**

Hadronotus grenadensis Ashmead, 1896: 800 (original description); Ashmead, 1900: 328 (distribution); Kieffer, 1926: 454, 466 (description, keyed).
Gryon grenadensis (Ashmead): Masner, 1965: 76 (type information, generic transfer); Masner, 1976: 58 (description, systematic position).
Gryon grenadense (Ashmead): Johnson, 1992: 384 (cataloged, type information).

Comments. We transfer this species based on characters in the original description, "Facial impression transversely striated, margined."

***Hadronotus hectoris* (Mineo), comb. nov.**

Gryon hectore Mineo, 1992: 25 (original description).

Comments. We transfer this species to *Hadronotus* based on characters presented in the original description, "frontal depression that is moderately large and deep, finely enframed and densely striated."

***Hadronotus helavai* (Masner), comb. nov.**
Holotype images: https://cnc.agr.gc.ca/taxonomy/Specimen.php?id=2954

Gryon helavai Masner, 1979: 793, 797 (original description, keyed); Sarazin, 1986: 974 (type information); Johnson, 1992: 384 (cataloged, type information).

***Hadronotus hercules* (Masner), comb. nov.**
Holotype images: https://cnc.agr.gc.ca/taxonomy/Specimen.php?id=2955

Gryon hercules Masner, 1979: 793, 801 (original description, keyed); Sarazin, 1986: 974 (type information); Johnson, 1992: 384 (cataloged, type information).

***Hadronotus hiberus* Nixon, comb. rev.**

Hadronotus hiberus Nixon, 1934b: 292, 299 (original description, keyed); Risbec, 1950: 592 (keyed).
Gryon hiberus (Nixon): Masner, 1965: 76 (type information, generic transfer); Mineo, 1990b: 49 (description, assigned to *hiberus* species group); Johnson, 1992: 384 (cataloged, type information).

Comments. We transfer this species to *Hadronotus* based on characters from the original description, "Frons with a fairly deep, more or less oval impression which is sharply and completely margined."

***Hadronotus hidakae* (Mineo), comb. nov.**

Gryon hidakae Mineo, 1980b: 218, 220 (original description, keyed); Johnson, 1992: 384 (cataloged, type information); Kononova & Petrov, 2002: 56 (keyed); Kononova & Kozlov, 2008: 331, 420 (description, keyed).

Comments. We transfer this species based on the sculpturing of the frontal depression, illustrated in Figure II-1 in the original description.

***Hadronotus hilaris* (Mineo), comb. nov.**
Holotype images: https://zenodo.org/record/4505098#.YByOT3lOlaQ

Gryon hilare Mineo, Mineo & Caleca, 1994: 115 (original description, assigned to *aureum* group).

***Hadronotus hirsutioculus* Girault, comb. rev.**

Hadronotus hirsutioculus Girault, 1925: 183 (original description).
Gryon hirsutioculus (Girault): Galloway, 1976: 91 (type information, generic transfer).
Gryon hirsutioculum (Girault): Mineo, 1990a: 186 (emendation, type information, systematic position); Johnson, 1992: 384 (cataloged, type information); Mineo & Caleca, 1994: 114 (assigned to *hirsutioculum* group).
Gryon hyrsutioculum (Girault): Mineo, 1991: 39 (description, misspelling).

Comments. We transfer this species back to *Hadronotus* based on characters in the original description, "face bounded by an arched carina above" and "vertex is also more rudely punctured."

***Hadronotus histricus* (Mineo), comb. nov.**
Holotype images: https://zenodo.org/record/4505129#.YByPoXlOlaQ

Gryon histricum Mineo, 1991: 7 (original description, assigned to *aureum* species group).

***Hadronotus hogenakalensis* (Sharma), comb. nov.**
Figure 10; Holotype images in MBD: USNMENT01197123

Gryon hogenakalensis Sharma, 1982: 329, 336 (original description, keyed); Lê, 1997: 23 (keyed); Lê, 2000: 99, 118 (description, keyed, type information).
Gryon hogenakalense Sharma: Johnson, 1992: 384 (cataloged).

***Hadronotus hystericus* (Mineo), comb. nov.**
Holotype images: https://zenodo.org/record/4505269#.YBySF3lOlaQ

Gryon hystericum Mineo, 1991: 16 (original description, assigned to *leptocorisae* species group).

***Hadronotus ialokombae* (Mineo), comb. nov.**
Holotype images: https://zenodo.org/record/4505332#.YByTGHlOlaQ

Gryon ialokombae Mineo, 1983c: 547, 551 (original description, keyed); Mineo, 1990a: 181 (description); Johnson, 1992: 385 (cataloged, type information).

***Hadronotus iammancoi* (Mineo), comb. nov.**
Holotype images: https://zenodo.org/record/4505360#.YByT-3lOlaQ

Gryon iammancoi Mineo, 1983s: 530, 546 (original description, keyed); Johnson, 1992: 385 (cataloged); Kononova & Kozlov, 2008: 329, 403 (description, keyed).

***Hadronotus iasonis* (Mineo), comb. nov.**
Paratype images: https://zenodo.org/record/5018397#.YNnQpElKhaQ

Gryon iasone Mineo, 1992: 21 (original description).

Comments. The original description is brief and does little to place this species. However, Mineo (1992) placed in the *leptocorisae* species group, which leads us to transfer it to *Hadronotus*, and the paratype specimen we examined belongs in *Hadronotus*.

***Hadronotus indicus* (Subba Rao & Chacko), comb. nov.**

Hadrophanurus indicus Subba Rao & Chacko, 1962: 478–479 (original description, keyed)
Gryon indicum (Subba Rao & Chacko): Johnson, 1992: 385 (cataloged, type information).

Comments. We transfer this species based on characters from the original description, "frons with a shallow depression having transverse striations and a small keel between the base of the antennae."

***Hadronotus ingens* (Veenakumari & Rajmohana), comb. nov.**

Gryon ingens Veenakumari & Rajmohana, 2016: 44 (original description).

Comments. The transfer to *Hadronotus* is based on characters and figures in the original description.

***Hadronotus insularis* Ashmead, comb. rev.**
Lectotype images in MBD: USNMENT01335839

Hadronotus insularis Ashmead, 1894: 229, 230 (original description, keyed); Ashmead, 1900: 328 (distribution); Kieffer, 1926: 454, 465 (description, keyed).
Gryon insularis (Ashmead): Masner, 1975: 212 (keyed); Masner, 1976: 58 (type information, description); Mineo, 1979a: 251 (description); Mineo, 1980a: 197 (junior synonym of *Gryon leptocorisae* (Howard)).
Gryon insulare (Ashmead): Masner, 1983: 134, 161 (description, emendation, keyed); Johnson, 1992: 385 (cataloged, type information).

Lectotype designation. We here designated specimen USNMENT01338539 as the lectotype of this species.

Hadronotus introversus (Mineo), comb. nov.

Gryon introversum Mineo, 1991: 14 (original description, assigned to *introversum* species group).

Comments. We transfer this species based on characters in the original description, "mandibles with 3 subequal teeth" and "epomia... complete", and images of the head provided in Figure IV.

Hadronotus janus Nixon, comb. rev.

Hadronotus janus Nixon, 1934b: 292, 304 (original description, keyed); Risbec, 1950: 592 (keyed).
Gryon janus (Nixon): Masner, 1965: 76 (type information, generic transfer); Masner, 1976: 58 (taxonomic status); Mineo, 1983c: 532, 546 (description, keyed); Johnson, 1992: 385 (cataloged, type information); Kononova & Kozlov, 2008: 331, 422 (description, keyed).

Comments. We transfer this species back to *Hadronotus* based on the original description, "A species closely related to *H. cous*" and "Mesonotum...quite strongly rugose."

Hadronotus japonicus Ashmead, comb. rev.

Holotype images in MBD: USNMENT00989857

Hadronotus japonicus Ashmead, 1904c: 74 (original description); Kieffer, 1926: 453, 460 (description, keyed).
Gryon japonicus (Ashmead): Masner & Muesebeck, 1968: 35 (type information, generic transfer); Mineo, 1979a: 252 (description).
Gryon japonicum (Ashmead): Mineo, 1981a: 119, 130 (description of male, emendation, keyed); Johnson, 1992: 385 (cataloged, type information); Lê, 2000: 99, 119 (description, keyed); Kononova & Kozlov, 2008: 331, 421 (description, keyed).

Gryon mischa Kozlov & Kononova, 1989: 80, 94 (original description, keyed); Kozlov & Kononova, 1990: 268, 294 (description, keyed); Johnson, 1992: 388 (cataloged, type information); Kononova, 1995: 85 (keyed); Kononova & Petrov, 2002: 56 (keyed); Kononova & Kozlov, 2008: 330, 413 (description, keyed); Komeda, Mita, Hirose & Yamagishi, 2020: 106 (junior synonym of *Gryon japonicum* (Ashmead)).

***Hadronotus javensis* Dodd, comb. rev.**

Hadronotus javensis Dodd, 1914e: 162 (original description); Dodd, 1915: 19 (keyed); Kieffer, 1926: 454, 460 (description, keyed).
Gryon javense (Dodd): Johnson, 1992: 385 (cataloged, type information).

Comments. We return this species to *Hadronotus* based on the original description, "Head and thorax reticulately rugulose."

***Hadronotus karnalensis* (Chacko & Katiyar), comb. nov.**

Hadrophanurus karnalensis Chacko & Katiyar, 1961: 161 (original description); Subba Rao & Chacko, 1962: 479 (keyed).
Gryon karnalense Chacko & Katiyar: Johnson, 1992: 385 (cataloged).

Comments. We transfer this species based on the original description, "frons with a median longitudinal shallow depression with transverse striations and with a keel at the base of the antennae."

***Hadronotus kelnerpillauti* (Mineo), comb. nov.**
Holotype images: https://zenodo.org/record/4507021#.YB1ab3lOlaQ

Gryon kelnerpillauti Mineo, 1983b: 286, 287 (original description, keyed); Johnson, 1992: 386 (cataloged, type information).

***Hadronotus kenyotus* (Mineo), comb. nov.**
Paratype images: https://zenodo.org/record/5018401#.YNnQgklKhaQ

Gryon kenyotum Mineo, 1982b: 304 (original description); Mineo, 1990c: 90 (keyed); Johnson, 1992: 386 (cataloged, type information); Mineo, 1992: 17 (assignment to *letus* species group).

Comments. This species belongs in *Hadronotus* based on examination of a paratype specimen as well as characters from the original description, "The series of basiconic-

type sensilla, lying on the middle of the ventral surface of the antennomeres A12-A7 is 2,2,2,2,2,0. Frontal depression enframed all round, its upper side connected to the median ocellus by a ledge."

***Hadronotus kozlovi* (Özdikmen), comb. nov.**
Holotype images: https://zenodo.org/record/5600460#.YXgfFfnMJaQ

Gryon oculatum Kozlov & Kononova, 2004: 205 (original description); Kononova & Kozlov, 2008: 325, 360 (description, keyed).
Gryon kozlovi Özdikmen, 2011: 772 (replacement name for *Gryon oculatum* Kozlov & Kononova); Timokhov, 2019a: 19 (distribution).

Comments. Figure 3–8 of the original description illustrates a female antenna with five clavomeres.

***Hadronotus krishnagiriensis* (Sharma), comb. nov.**
Holotype images in MBD: USNMENT01109961

Gryon krishnagiriensis Sharma, 1982: 333, 336 (original description, keyed).
Gryon krishnagiriense Sharma: Johnson, 1992: 386 (cataloged).

***Hadronotus laticeps* Kieffer, comb. rev.**

Hadronotus laticeps Kieffer, 1908: 144 (original description); Kieffer, 1926: 453, 457 (description, keyed).
Hadronotus Laticeps Kieffer: Kieffer, 1913: 240 (description).
Gryon laticeps (Kieffer): Johnson, 1992: 386 (cataloged, type information).

Comments. We transfer this species based on the original description, "superficial frontal impression, going beyond the middle of the eyes, dull, not marginal, ridged across."

***Hadronotus latipennis* (Dodd), comb. nov.**
Holotype images in MBD: SAMA I.1396

Platyteleia latipennis Dodd, 1913a: 154 (original description); Dodd, 1914b: 80 (description of female); Kieffer, 1926: 409 (description, keyed); Galloway, 1976: 101 (type information).
Gryon latipennis (Dodd): Galloway & Austin, 1984: 79 (generic transfer).
Gryon latipenne (Dodd): Johnson, 1992: 386 (cataloged, type information).

***Hadronotus latus* (Dodd) comb.n.**

Austroscelio latus Dodd, 1916: 28 (original description); Galloway, 1976: 85 (type information).
Gryon latus (Dodd): Galloway & Austin, 1984: 80 (generic transfer).
Gryon latum (Dodd): Mineo, 1990b: 52 (assigned to *insulare* species group, type information); Johnson, 1992: 386 (cataloged, type information).

Comments. We transfer this species into *Hadronotus* based on the original description, "Head...with rather shallow open raised reticulation, the lower half or more of face rather shallowly depressed and transversely striate."

***Hadronotus leptocorisae* Howard, comb. rev.**
Lectotype images in MBD: USNMENT00989859
Neolectotype images in MBD: USNMENT00989860

Hadronotus leptocorisae Howard, in Hubbard 1885: 215 (original description); Ashmead, 1893: 230, 231 (description, keyed); Brues, 1910: 47 (keyed); Kieffer, 1926: 454, 462 (description, keyed).
Hadronotus hungaricus Szabó, 1966: 430, 433 (original description, keyed. Preoccupied by *Hadronotellus hungaricus* Szabó (1966) and *Pannongryon hungaricum* Szabó (1966). Synonymized by Mineo (1980)); Johnson, 1992: 386 (type information).
Gryon leptocorisae (Howard): Muesebeck & Masner, 1967: 299 (generic transfer); Masner & Muesebeck, 1968: 36 (lectotype designation); Mineo, 1980a: 197 (synonymy); Mineo, 1981a: 119, 132 (variation, keyed); Masner, 1983: 154 (description); Mineo, 1990b: 52 (assigned to *leptocorisae* species group); Johnson, 1992: 386 (cataloged, type information); Mineo & Caleca, 1994: 122 (distribution); Kononova & Kozlov, 2008: 326, 370 (description, keyed); Talamas, Thompson, Cutler, Schoenberger, Cuminale, Jung, Johnson, Valerio, Smith, Haltermann, Alvarez, Schwantes, Blewer, Bodenreider, Salzberg, Luo, Meislin & Buffington, 2017b: 199 (neotype designation); Timokhov, 2019b: 47 (catalog of species of Russia).
Gryon reduviophagus Kozlov, 1971: 48 (original description. Synonymized by Mineo (1979a)); Viggiani & Mineo, 1974: 154, 160 (diagnosis, keyed); Kozlov, 1978: 620 (description); Mineo, 1979a: 257 (junior synonym of *Gryon hungaricus* (Szabó)); Kozlov & Kononova, 1989: 79 (keyed); Kozlov & Kononova, 1990: 267, 285 (description, keyed); Johnson, 1992: 387 (cataloged, type information); Kononova, 1995: 84 (keyed); Kononova & Petrov, 2002: 54 (keyed).

***Hadronotus leptoglossi* (Mineo & Caleca), comb. nov.**
Holotype images: https://zenodo.org/record/4507209#.YB1e5nlOlaQ

Gryon leptoglossi Mineo & Caleca, 1987a: 35 (original description); Johnson, 1992: 387 (cataloged).

***Hadronotus letus* Nixon, comb. rev.**
Syntype images: https://zenodo.org/record/4507293#.YB1hPXlOlaQ

Hadronotus letus Nixon, 1934b: 292, 309 (original description, keyed); Risbec, 1950: 592 (keyed).
Gryon letus (Nixon): Masner, 1965: 77 (type information, generic transfer); Mineo, 1982b: 306 (description); Mineo, 1990c: 90 (keyed); Johnson, 1992: 387 (cataloged, type information).

***Hadronotus linshcostei* (Masner), comb. nov.**
Holotype images: https://zenodo.org/record/4507540#.YB1n13lOlaQ

Gryon linshcostei Masner, 1975: 211, 213 (original description, keyed); Sarazin, 1986: 975 (type information); Johnson, 1992: 387 (cataloged, type information).

***Hadronotus longicornis* (Dodd), comb. nov.**
Holotype images: https://zenodo.org/record/4507654#.YB1s4HlOlaQ

Plastogryon longicornis Dodd, 1915: 25 (original description, keyed).
Gryon longicornis (Dodd): Galloway, 1976: 91 (type information, generic transfer).
Gryon longicorne (Dodd): Mineo, 1990a: 185 (emendation, type information); Johnson, 1992: 387 (cataloged, type information).

***Hadronotus longus* (Kozlov & Lê), comb. nov.**
Holotype images in MBD: IEBR 0165

Gryon longum Kozlov & Lê, 1992: 228, 236 (original description, assigned to *muscaeforme* species group, keyed).
Gryon longus Kozlov & Lê, 1996: 11 (description); Lê, 2000: 98, 121 (description, keyed, type information).

***Hadronotus lucmon* (Mineo), comb. nov.**
Holotype images: https://zenodo.org/record/4507771#.YB1u_nlOlaQ

Gryon lucmon Mineo, 1992: 19 (original description).

***Hadronotus magnoculo* (Mineo), comb. nov.**
Holotype images: https://zenodo.org/record/4507836#.YB1wSXlOlaQ

Gryon magnoculo Mineo, 1983c: 547, 551 (original description, keyed); Johnson, 1992: 387 (cataloged, type information).

***Hadronotus longipennis* (Masner), comb. nov.**
Holotype images in MBD: CNC No. 17014

Gryon longipenne Masner, 1983: 134, 156 (original description, keyed); Sarazin, 1986: 975 (type information); Johnson, 1992: 387 (cataloged, type information).
Gryon masneri Özdikmen: Özdikmen, 2011: 772 (replacement name for *Gryon longipenne* Masner).

Comments. The transfer of this species to *Hadronotus* makes the replacement name unnecessary. However, it should be noted that the generic placement of *Gryon longipenne* (Dodd) is dubious and that it could be transferred to *Hadronotus* in the future. In this case, the replacement name would be reinstated, making this species *Hadronotus masneri* (Özdikmen).

***Hadronotus masoni* (Masner), comb. nov.**
Holotype images: https://cnc.agr.gc.ca/taxonomy/Specimen.php?id=2956

Gryon masoni Masner, 1979: 794, 800 (original description, keyed); Sarazin, 1986: 976 (type information); Johnson, 1992: 388 (cataloged, type information).

***Hadronotus meridianus* (Dodd), comb. nov.**
Holotype images: https://zenodo.org/record/4507953#.YB1zkXlOlaQ

Hadronotoides meridianus Dodd, 1914c: 101 (original description); Kieffer, 1926: 474, 475 (description, keyed); Galloway, 1976: 92 (type information); Johnson, 1992: 399 (cataloged, type information); Naumann, Cardale, Taylor & MacDonald, 1994: 71 (holotype, allotype transferred to ANIC).
Gryon meridianum (Dodd): Caleca, 1990: 119, 122 (description, generic transfer, keyed).

***Hadronotus mirperusi* (Risbec), comb. rev.**
Holotype images: https://zenodo.org/record/4508988#.YB2N2GFKhaQ

Hadronotus mirperusi Risbec, 1950: 592, 595 (original description, keyed).

Gryon mirperusi (Risbec): Masner, 1976: 58 (generic transfer, type information); Mineo, 1983b: 286, 288 (description, keyed); Johnson, 1992: 388 (cataloged, type information).

***Hadronotus mnemosynis* (Mineo), comb. nov.**
Paratype images: https://zenodo.org/record/5018405#.YNnQU0lKhaQ

Gryon mnemosyne Mineo, 1992: 19 (original description)

Comments. The original description is extremely short and insufficient for generic placement. We transfer this species to *Hadronotus* based on examination of a paratype specimen and because Mineo (1992) treated it as part of the *hiberus* group which, to the extent that we have examined primary types directly, is comprised entirely of *Hadronotus* species.

***Hadronotus molinai* Blanchard, comb. rev.**

Hadronotus molinai Blanchard, 1927: 598 (original description).
Gryon molinai (Blanchard): De Santis & Esquivel, 1966: 50 (generic transfer); Loiácono, 1980: 175 (description); Johnson, 1992: 389 (cataloged, type information).

Comments. We transfer this species based on characters from the original description, "Head and face with polygonal reticulations. Mesonotum and scutellum strongly and coarsely punctate, assuming at caudal margin of mesonotum a slightly longitudinal direction." Figures of this species illustrate coarse sculpturing on the frons.

***Hadronotus morosus* (Mineo), comb. nov.**
Paratype images: https://zenodo.org/record/5037813#.YNoNKUlKhaQ

Gryon morosum Mineo, 1983a: 15, 21 (original description, keyed); Johnson, 1992: 390 (cataloged, type information).

Comments. We transfer this species based on illustrations in the original description and its assignment to the *charon* species group, as well as our examination of a paratype specimen.

***Hadronotus mudugeriensis* Sharma, comb. nov.**
Holotype images in MBD: USNMENT01109969

Gryon mudugeriense Sharma, 1982: 334, 336 (original description, keyed); Johnson, 1992: 390 (cataloged).

***Hadronotus muscaeformis* (Nees von Esenbeck), comb. rev.**

Teleas muscaeformis Nees von Esenbeck, 1834: 290 (original description); Graham, 1988: 28 (type information).

Hadronotus muscaeformis (Nees von Esenbeck): Mayr, 1879: 698 (generic transfer, description); Kieffer, 1926: 453, 459 (description, keyed); Szabó, 1966: 430–431 (description, synonymy, lectotype designation, keyed); Hellén, 1971: 22 (description).

Hadronotus pubescens Kieffer, 1909: 269 (original description. Synonymized by Mineo (1981)); Kieffer, 1926: 453, 458 (description, keyed); Bin, 1974: 455 (type information); Mineo, 1981: 138 (type information).

Hadronotus Pubescens Kieffer: Kieffer, 1913: 241 (description).

Hadronotus Muscaeformis (Nees von Esenbeck): Kieffer, 1913: 243 (description).

Gryon muscaeformis (Nees von Esenbeck): Kozlov, 1971: 47 (generic transfer, distribution, host association); Viggiani & Mineo, 1974: 149, 160, 161 (description, keyed); Kozlov, 1978: 620 (keyed); Mineo, 1981: 120, 134 (synonymy, keyed); Kozlov & Kononova, 1989: 78 (keyed); Kozlov & Kononova, 1990: 266, 269 (description, keyed); Johnson, 1992: 390 (cataloged); Kononova & Petrov, 2002: 54 (keyed).

Gryon muscaeforme (Nees von Esenbeck): Kononova & Kozlov, 2008: 325, 365 (description, keyed); Timokhov, 2019b: 48 (catalog of species of Russia).

Comments. We transfer this species based on the description of the lectotype designated by Szabó (1966), "Head... wrinkled fine and dense leather-like dots everywhere, except for the striated forehead impression."

***Hadronotus myndus* Nixon, comb. rev.**

Paratype images: https://zenodo.org/record/5110092#.YPGnw-hKhaQ

Hadronotus myndus Nixon, 1934b: 292, 309 (original description, keyed); Risbec, 1950: 592 (keyed).

Hadronotus Benoiti Risbec, 1958: 116 (original description. Synonymized by Mineo (1990a)); Mineo, 1990a: 177 (diagnosis, synonymy); Johnson, 1992: 390 (type information).

Gryon myndus (Nixon): Masner, 1965: 77 (type information, generic transfer); Mineo, 1990a: 177 (diagnosis, synonymy); Johnson, 1992: 390 (cataloged, type information).

Gryon benoiti (Risbec): Masner, 1976: 58 (generic transfer).

***Hadronotus naevius* Nixon, comb. rev.**

Holotype images: https://zenodo.org/record/4509106#.YB2RLHlOlaQ

Hadronotus naevius Nixon, 1934b: 292, 311 (original description, keyed); Risbec, 1950: 592, 597 (description, keyed).

Gryon naevius (Nixon): Masner, 1965: 77 (type information, generic transfer); Mineo, 1990a: 177 (variation).

Gryon naevium (Nixon): Johnson, 1992: 390 (cataloged, type information).

***Hadronotus narus* (Kozlov & Lê), comb. nov.**
Holotype images in MBD: USNMENT01197908

Gryon narum Kozlov & Lê, 1992: 228, 237 (original description, assigned to *muscaeforme* species group, keyed).
Gryon narus Kozlov & Lê, 1996: 11 (description); Lê, 2000: 99, 127 (description, keyed, type information).

***Hadronotus neglectus* (Mineo), comb. nov.**
Holotype images: https://zenodo.org/record/4509207#.YB2UDnlOlaQ

Gryon neglectum Mineo, 1979c: 270 (original description); Mineo, 1980b: 222, 224 (description, keyed); Johnson, 1992: 390 (cataloged, type information); Kononova & Petrov, 2002: 56 (keyed); Kononova & Kozlov, 2008: 330, 412 (description, keyed).

***Hadronotus neotropicus* (Masner), comb. nov.**

Gryon neotropicus Masner, 1979: 804, 792 (original description, keyed)

Comments. We transfer this species based on its placement in the *variicorne* species group and characters in the original description, "...frontal depression very shallow with strongly transverse polygons, not particularly margined at sides nor above… frons along inner orbits and vertex with large polygons."

***Hadronotus nereus* (Mineo), comb. nov.**
Holotype images: https://zenodo.org/record/4509257#.YB2Vl3lOlaQ

Gryon nereum Mineo, 1994: 118 (original description, assigned to *insulare* group).

***Hadronotus nicolai* (Mineo), comb. nov.**
Holotype images: https://zenodo.org/record/4509338#.YB2YIXlOlaQ

Gryon nicolai Mineo, 1979a: 258 (original description); Mineo, 1981a: 119 (keyed); Johnson, 1992: 391 (cataloged, type information); Kononova & Petrov, 2002: 54 (keyed); Mineo, 2004a: 175 (description, distribution in Sicily); Kononova & Kozlov, 2008: 324, 357 (description, keyed).

***Hadronotus nigriclavatus* (Dodd), comb. rev.**

Holotype images: https://zenodo.org/record/4509350#.YIHgQaEpBaQ

Hadronotus nigriclavatus Dodd, 1913a: 178 (original description); Dodd, 1915: 19 (keyed); Kieffer, 1926: 455, 470 (description, keyed).
Gryon nigriclavatus (Dodd): Galloway, 1976: 92 (type information, generic transfer).
Gryon nigriclavatum (Dodd): Mineo, 1990b: 57 (description, type information); Johnson, 1992: 391 (cataloged, type information); Mineo, 1992: 17 (assignment to *letus* species group).

***Hadronotus nigricornis* (Dodd), comb. rev.**

Telenomoides nigricornis Dodd, 1913a: 170, 171 (original description, keyed).
Hadronotus nigricornis (Dodd): Dodd, 1914a: 129 (generic transfer); Dodd, 1915: 19 (keyed); Kieffer, 1926: 456, 472 (description, keyed); Galloway, 1976: 111 (type information, status uncertain).
Hadronotus fellah Priesner, 1951: 131 (original description. Synonymized by Mineo (1990a)); Mineo, 1990a: 182 (junior synonym of *Gryon nigricorne* (Dodd)); Johnson, 1992: 391 (type information).
Gryon fellah (Priesner): Mineo, 1979a: 246 (description of male, generic transfer, type information); Mineo, 1980b: 222, 223 (description, keyed).
Gryon nigricorne (Dodd): Mineo, 1990a: 182 (synonymy, generic transfer, emendation); Johnson, 1992: 391 (cataloged, type information); Mineo & Caleca, 1994: 115 (distribution, biology); Kononova & Kozlov, 2008: 331, 416 (description, keyed, synonymy).
Gryon incrassatum Kononova & Fursov: Kononova & Fursov, 2005a: 592 (original description); Kononova & Fursov, 2005b: 301 (description); Kononova & Kozlov, 2008: 416 (junior synonym of *Gryon nigricorne* (Dodd)).

Comments. The original description is of no use for placing this species in either *Gryon* or *Hadronotus*. Mineo (1990) illustrated a female antenna of this species as having five clavomeres but did not clarify if this was the holotype specimen. He mentioned that type material was examined but did not clarify if this was type material of *H. fellah*, *H. nigricornis*, or both. *Hadronotus fellah* clearly belongs in *Hadronotus* based on images of the holotype (USNMENT01059669). However, *H. fellah* was described from Egypt, and while it is possible that *H. fellah* and *H. nigricornis* are conspecific, we consider it prudent to reexamine this synonymy.

***Hadronotus nigricoxus* Dodd, comb. rev.**

Hadronotus nigricoxa Dodd, 1913a: 179 (original description); Dodd, 1914d: 19 (keyed); Kieffer, 1926: 455, 473 (description, keyed); Galloway & Austin, 1984: 94 (type information, status uncertain); Johnson, 1992: 511 (cataloged, type information).

Gryon nigricoxa (Dodd): Mineo, 1990b: 56 (description, type information); Mineo, 1992: 17 (assignment to *letus* species group).

Comments. The original description is inadequate for determining the genus to which this species belongs. All that remains of the holotype specimen of *H. nigricoxa* is a slide mounted fore wing. The body of the holotype was examined by Mineo (1990b), who considered it to be close to *Gryon letus*. This forms our basis for transferring the species to *Hadronotus*.

***Hadronotus nigripes* Dodd, comb. rev.**
Holotype images: https://zenodo.org/record/4509632#.YJmiKKEpBaQ

Hadronotus nigripes Dodd, 1914a: 129 (original description); Dodd, 1915: 19 (keyed); Kieffer, 1926: 456, 472 (description, keyed).
Gryon nigripes (Dodd): Galloway, 1976: 92 (type information, generic transfer); Mineo, 1990b: 57 (type information); Johnson, 1992: 391 (cataloged, type information).

***Hadronotus niger* (Dodd), comb. nov.**
Holotype images: https://zenodo.org/record/4509640#.YB24qXlOlaQ

Plastogryon niger Dodd, 1914f: 257 (original description).
Plastogryon niger niger Dodd: Dodd, 1915: 25 (keyed).
Plastogryon niger rubrifemur Dodd, 1915: 25, 26 (original description, keyed); Johnson, 1992: 391 (type information).
Plastogryon (*Heterogryon*) *niger* Dodd: Kieffer, 1926: 447, 450 (description, subgeneric assignment, keyed).
Gryon niger (Dodd): Galloway, 1976: 92 (type information, generic transfer); Masner, 1976: 58 (generic transfer).
Gryon niger rubrifemur (Dodd): Galloway, 1976: 92 (type information, generic transfer).
Gryon nigrum (Dodd): Mineo, 1990b: 54 (distribution); Johnson, 1992: 391 (cataloged, type information).

***Hadronotus nigroides* (Subba Rao & Chacko), comb. nov.**
Hadrophanurus nigroides Subba Rao & Chacko, 1962: 477–479 (original description, keyed).
Gryon nigroides (Subba Rao & Chacko): Johnson, 1992: 392 (cataloged, type information).

Comments. We transfer this species based on the original description, "...frons with a very shallow area having transverse striations and a small keel at the base

of the antennae... Mandible threedentate... mesonotum pitted and aciculate in between the pits."

***Hadronotus nudus* (Mineo), comb. nov.**
Holotype images: https://zenodo.org/record/4509650#.YB26NXlOlaQ

Gryon nudum Mineo, 1994: 118 (original description, assigned to *insulare* group).

***Hadronotus obesus* (Masner), comb. nov.**
Holotype images: https://zenodo.org/record/4509675#.YB29o3lOlaQ

Gryon obesum Masner, 1983: 134, 158 (original description, keyed); Johnson, 1992: 392 (cataloged, type information); Talamas, Johnson & Buffington, 2015: 52 (keyed).

***Hadronotus obtusus* (Kozlov & Kononova), comb. nov.**
Holotype images: https://zenodo.org/record/5600445#.YXgdAPnMJaQ

Gryon obtusum Kozlov & Kononova, 2004: 203, 206 (original description); Kononova & Kozlov, 2008: 325, 368 (description, keyed); Timokhov, 2019b: 48 (catalog of species of Russia).

***Hadronotus oculatus* (Mineo), comb. nov.**
Holotype images: https://zenodo.org/record/4519481#.YCFaQHlOlaQ

Gryon oculatum Mineo, 1983c: 548, 551 (original description, keyed); Johnson, 1992: 392 (cataloged, type information).

***Hadronotus odontogonusi* (Risbec), comb. nov.**
Lectotype images: https://zenodo.org/record/4519522#.YCFcEXlOlaQ

Anteromorpha odontogonusi Risbec, 1955: 199 (original description); Risbec, 1957: 147 (keyed).
Gryon odontogonusi (Risbec): Mineo, 1980b: 214 (type information, generic transfer); Mineo, 1990b: 50 (description, lectotype designation, assigned to *hiberus* species group); Johnson, 1992: 392 (cataloged, type information).

***Hadronotus onorei* (Mineo), comb. nov.**
Holotype images: https://zenodo.org/record/4519537#.YCFhpnlOlaQ

Gryon onorei Mineo, 1994: 122 (original description, assigned to *leptocorisae* group).

***Hadronotus oophagus* Nixon, comb. nov.**

Hadronotus oophagus Nixon, 1934a: 3–4, 2 (original description, keyed).

Comments. The key to species in the original description provides a character that enables us tro transfer this species to *Hadronotus*, "Frontal impression completely margined by a sharply defined ridge."

***Hadronotus oresteus* (Mineo), comb. nov.**

Gryon oresteum Mineo, 1992: 22 (original description)

Comments. We transfer this species to *Hadronotus* based on the original description, which stated that this species was close to *H. orestes* (junior synonym of *H. flavipes*) and described the sculpture of the frontal depression as "the transverse striae are fine and very compact each other."

***Hadronotus oxitomus* (Kononova), comb. nov.**

Gryon oxitomum Kononova: Kononova, Pavlicek & Nevo, 2005: 813 (description); Kononova, Pavlicek & Nevo, 2005: 1355 (original description); Kononova & Kozlov, 2008: 322, 339 (description, keyed).

Comments. Figure 3–1 in the original description illustrates a frons that is coarsely sculptured and has transverse striation in the frontal depression.

***Hadronotus pappi* (Mineo), comb. nov.**

Holotype images: https://zenodo.org/record/4519608#.YCFjR3lOlaQ

Gryon pappi Mineo, 1983c: 537, 546 (original description, keyed); Johnson, 1992: 393 (cataloged, type information).

***Hadronotus paracharontis* (Mineo), comb. nov.**

Holotype images: https://zenodo.org/record/4519618#.YCFjI3lOlaQ

Gryon paracharontis Mineo, 1982b: 307 (original description); Mineo, 1983a: 18 (keyed); Johnson, 1992: 393 (cataloged, type information).

***Hadronotus paracous* (Mineo), comb. nov.**
Holotype images: https://zenodo.org/record/4519703#.YCFmDXlOlaQ

Gryon paracoum Mineo, 1983c: 538, 546 (original description, keyed); Sarazin, 1986: 977 (type information); Johnson, 1992: 393 (cataloged, type information).

***Hadronotus parakenyotus* (Mineo), comb. nov.**
Holotype images: https://zenodo.org/record/4519733#.YCFo93lOlaQ

Gryon parakenyotum Mineo, 1990c: 90 (original description, keyed).

***Hadronotus parasomaliensis* (Mineo), comb. nov.**
Holotype images: https://zenodo.org/record/4519751#.YCFp9XlOlaQ

Gryon parasomaliense Mineo, 1983c: 539, 546 (original description, keyed); Sarazin, 1986: 978 (type information); Johnson, 1992: 393 (cataloged, type information).

***Hadronotus pecki* (Mineo), comb. nov.**
Holotype images in MBD: CNC No. 21408

Gryon pecki Mineo, 1990a: 176 (original description); Johnson, 1992: 393 (cataloged, type information).

***Hadronotus peckorum* (Masner), comb. nov.**
Holotype images: https://cnc.agr.gc.ca/taxonomy/Specimen.php?id=2958

Gryon peckorum Masner, 1979: 793, 803 (original description, keyed); Sarazin, 1986: 978 (type information); Johnson, 1992: 393 (cataloged, type information).

***Hadronotus pennsylvanicus* (Ashmead), comb. nov.**
Figure 12; Holotype images: https://zenodo.org/record/4520251#.YCGBzXlOlaQ

?Telenomus pennsylvanicus Ashmead, 1893: 144, 160 (original description, keyed).
Hadronotus ajax Girault, 1920: 181 (original description. Synonymized by Masner (1983)); Masner, 1983: 146 (junior synonym of *Gryon pennsylvanicum* (Ashmead)); Johnson, 1992: 394 (type information).
Hadrophanurus pennsylvanicus (Ashmead): Kieffer, 1926: 130 (description, generic transfer).
Hadronotus atriscapus Gahan, 1927: 37 (original description. Synonymized with *Hadronotus ajax* Girault by Mineo (1980a), with *Telenomus pennsylvanicus* Ashmead,

by Masner (1983)); Mineo, 1980a: 189 (junior synonym of *Hadronotus ajax* Girault); Masner, 1983: 147 (junior synonym of *Gryon pennsylvanicum* (Ashmead)); Johnson, 1992: 394 (type information).

Gryon pennsylvanicus (Ashmead): Masner, 1961: 162 (description, generic transfer); Subba Rao & Chacko, 1962: 480 (keyed).

Gryon ajax (Girault): Muesebeck & Masner, 1967: 299 (generic transfer); Masner & Muesebeck, 1968: 34 (lectotype designation); Mineo, 1980a: 189 (synonymy).

Gryon atriscapus (Gahan): Muesebeck & Masner, 1967: 299 (generic transfer); Masner & Muesebeck, 1968: 34 (type information).

Gryon pennsylvanicum (Ashmead): Masner, 1983: 134, 146 (description, synonymy, emendation, keyed); Mineo & Caleca, 1987a: 33 (description); Johnson, 1992: 394 (cataloged, type information); Kononova & Kozlov, 2008: 331, 419 (description, keyed).

***Hadronotus pentatomus* Dodd, comb. rev.**

Holotype images in MBD: SAMA DB 32-001664

Hadronotus pentatomus Dodd, 1913a: 154 (original description).

Hadronotoides pentatomus (Dodd): Dodd, 1913b: 171 (generic transfer); Kieffer, 1926: 474, 475 (description, keyed); Galloway, 1976: 92 (type information); Masner, 1976: 59 (description); Johnson, 1992: 400 (cataloged, type information).

Gryon pentatomum (Dodd): Caleca, 1990: 119, 125 (description, generic transfer, keyed).

***Hadronotus perthi* Mineo, comb. nov.**

Holotype images: https://zenodo.org/record/4520576#.YCGFAXlOlaQ

Gryon perthi Mineo, 1994: 114, 115 (original description, assigned to *hirsutioculum* group).

***Hadronotus pharaonis* (Mineo), comb. nov.**

Gryon pharaone Mineo, 1992: 24 (original description).

Comments. The original description is pitifully brief and lists only a few general color characters. Mineo (1992) considered this species to belong to the *hirsutioculum* group, which is our basis for transferring the species to *Hadronotus*.

***Hadronotus philippinensis* Ashmead, comb. rev.**

Lectotype image of *H. philippinensis* in MBD: USNMENT00989863; Holotype images of *H. hakonensis* in MBD: USNMENT00989856

Hadronotus philippinensis Ashmead, 1904b: 11 (original description); Ashmead, 1904d: 153 (distribution); Kieffer, 1926: 454, 460 (description, keyed); Baltazar, 1966: 183 (cataloged, type information, distribution).
Hadronotus hakonensis Ashmead, 1904c: 74 (original description); Kieffer, 1926: 453, 460 (description, keyed); Watanabe, 1951: 24, 25 (description, keyed).
Hadronotus homoeoceri Nixon, 1934: 4 (original description. Synonymized by Mineo (1979)); Mineo, 1979a: 260 (junior synonym of *Gryon philippinensis* (Ashmead)); Johnson, 1992: 394 (type information).
Hadronotus homoceri Nixon: Mani, 1941: 27 (spelling error).
Gryon homeoceri (Nixon): Masner, 1965: 76 (type information, generic transfer, spelling error); Mani & Sharma, 1982: 191 (description); Sharma, 1982: 331, 336 (description, keyed).
Gryon philippinensis (Ashmead): Masner & Muesebeck, 1968: 36 (lectotype designation, generic transfer).
Gryon hakonensis (Ashmead): Masner & Muesebeck, 1968: 35 (type information, generic transfer).
Gryon philippinense (Ashmead): Mineo, 1983a: 18, 21 (description, emendation, keyed); Mineo, 1990b: 48 (host information); Johnson, 1992: 394 (cataloged, type information); Lê, 2000: 98, 130 (description, keyed).
Gryon hakonense (Ashmead): Mineo, 1981a: 119, 129 (description, emendation, keyed); Johnson, 1992: 384 (cataloged, type information); Kononova & Kozlov, 2008: 442 (description); Komeda, Mita, Hirose & Yamagishi, 2020: 106 (junior synonym of *Gryon philippinensis* (Ashmead)).

***Hadronotus papuensis* (Caleca), comb. nov.**

Gryon papuense Caleca, 1990a: 119, 123 (original description, keyed).

Comments. Figures 28a–d in the original description clearly indicate that this species belongs in *Hadronotus*.

***Hadronotus pictus* (Mineo), comb. nov.**
Holotype images: https://zenodo.org/record/4509618#.YJLcA6EpBaQ

Plastogryon nigricornis Dodd, 1914b: 80 (original description); Dodd, 1915: 25 (keyed).
Plastogryon (*Heterogryon*) *nigricornis* Dodd: Kieffer, 1926: 446, 449 (description, subgeneric assignment, keyed).
Gryon nigricornis (Dodd): Galloway, 1976: 92 (type information, generic transfer).
Gryon pictum Mineo: Mineo, 1990b: 55 (replacement name for *Plastogryon nigricornis* Dodd, type information).
Gryon nigricorne (Dodd): Johnson, 1992: 391 (cataloged, type information).

***Hadronotus pisonis* (Mineo), comb. nov.**
Holotype images: https://zenodo.org/record/4520622#.YCGGJHlOlaQ

Gryon pisone Mineo, 1994: 118 (original description, assigned to *insulare* group).

***Hadronotus primus* (Kozlov & Kononova), comb. nov.**
Holotype images: https://zenodo.org/record/4531992#.YCQwc3lOlaQ

Gryon primum Kozlov & Kononova, 2004: 206 (original description); Kononova & Kozlov, 2008: 326, 371 (description, keyed); Timokhov, 2019b: 48 (catalog of species of Russia).

***Hadronotus pubescens* (Motschoulsky), comb. nov.**
Holotype images: https://zenodo.org/record/4924954#.YOSoF0lKhaQ

Muscidea pubescens Motschoulsky, 1863: 70 (original description).
Gryon pubescens (Motschoulsky): Masner, 1976: 57 (generic transfer, type information); Johnson, 1992: 395 (cataloged, type information).

***Hadronotus querulus* (Mineo), comb. nov.**

Gryon querulum Mineo, 1991: 17 (original description, assigned to *muscaeforme* species group);

Comments. Figure II in Mineo (1991) illustrates a female antenna that has five clavomeres and the description states that this species has "mandibles tridentate", "epomia reaching far from the tegula", "frons...with almost regular polygons; the same sculpture is found on the mesoscutum."

***Hadronotus radicularis* (Masner), comb. nov.**
Holotype images in MBD: CNC No. 17016

Gryon radiculare Masner, 1983: 134, 160 (original description, keyed); Sarazin, 1986: 978 (type information); Johnson, 1992: 395 (cataloged, type information).

***Hadronotus religiosus* (Mineo), comb. nov.**

Gryon religiosum Mineo, 1994: 130 (original description).

Comments. We transfer this species based on characters in the original description, "frontal depression deep and large, all over margined by keel; crossed by wide apart parallel striations; clava of 6 antennomeres." However, this description also mentions a character that requires further examination, "above malar groove a fan-like striation with wide apart striae."

***Hadronotus reticulatus* (Dodd), comb. rev.**

Hadronotus reticulatus Dodd, 1914c: 102 (original description).
Hadronotoides reticulatus (Dodd): Kieffer, 1926: 474, 475 (description, keyed); Galloway, 1976: 92 (type information); Johnson, 1992: 400 (cataloged, type information).
Gryon reticulatum (Dodd): Caleca, 1990: 119, 130 (description, generic transfer, keyed, lectotype designation).

Comments. Our transfer of this species is based on the original description, "Head, scutum and scutellum reather coarsely rugulose," as well as the description and illustration of the lectotype and inclusion in *pentatomum* group by Caleca (1990).

***Hadronotus rhinocori* (Risbec), comb. nov.**
Holotype images: https://zenodo.org/record/4520837#.YCGK9XlOlaQ

Paragryon rhinocori Risbec, 1950: 583 (original description).
Gryon rhinocori (Risbec): Masner, 1976: 58 (generic transfer, type information, systematic position); Johnson, 1992: 395 (cataloged, type information).

***Hadronotus robertae* (Mineo), comb. nov.**
Paratype images: https://zenodo.org/record/5037817#.YNoNBElKhaQ

Gryon robertae Mineo, 1981a: 119, 141 (original description, keyed); Johnson, 1992: 395 (cataloged, type information); Kononova & Petrov, 2002: 54 (keyed); Kononova & Kozlov, 2008: 324, 353 (description, keyed).

Comments. We transfer this species to *Hadronotus* based on Figure XXI in the original description and examination of a paratype specimen.

***Hadronotus robustus* (Dodd), comb. nov.**
Holotype images: https://zenodo.org/record/4521184#.YCGZ93lOlaQ

Austroscelio robustus Dodd, 1914c: 94 (original description); Kieffer, 1926: 473, 474 (description, keyed); Galloway, 1976: 85 (type information); Naumann, Cardale, Taylor & MacDonald, 1994: 71 (holotype transferred to ANIC).
Gryon robustus (Dodd): Galloway & Austin, 1984: 80 (generic transfer).
Gryon robustum (Dodd): Johnson, 1992: 395 (cataloged, type information); Mineo & Caleca, 1994: 117 (description, distribution).

***Hadronotus rothi* (Masner), comb. nov.**
Holotype images: https://zenodo.org/record/4521187#.YCGbKXlOlaQ

Gryon rothi Masner, 1979: 793, 797 (original description, keyed); Masner, 1983: 134, 151 (description, keyed); Johnson, 1992: 395 (cataloged, type information).

***Hadronotus rubriscapus* Dodd, comb. rev.**
Holotype images: https://zenodo.org/record/4521205#.YCGfhXlOlaQ

Hadronotus rubriscapus Dodd, 1915: 21 (original description).
Gryon rubriscapus (Dodd): Galloway, 1976: 92 (type information, generic transfer); Johnson, 1992: 395 (cataloged, type information).

***Hadronotus rufithorax* (Dodd), comb. rev.**
Holotype images: https://zenodo.org/record/4521209#.YInQhvlKhaQ; https://zenodo.org/record/4726161#.YInU7PlKhaQ

Hadronotus rufithorax Dodd, 1913b: 172 (original description).
Plastogryon nigriceps Dodd, 1914a: 125 (original description. Preoccupied by *Hadronotus nigriceps* Dodd (1914)); Dodd, 1915: 24 (keyed); Mineo, 1990b: 55 (junior synonym of *Gryon rufithorax* (Dodd)).
Plastogryon rufithorax (Dodd): Dodd, 1914a: 125 (generic transfer); Dodd, 1915: 24 (keyed).
Plastogryon (*Heterogryon*) *nigriceps* Dodd: Kieffer, 1926: 447, 450 (description, subgeneric assignment, keyed).
Plastogryon (*Heterogryon*) *rufithorax* (Dodd): Kieffer, 1926: 446, 449 (description, subgeneric assignment, keyed).
Gryon nigriceps (Dodd): Galloway, 1976: 92 (type information, generic transfer).
Gryon rufithorax (Dodd): Galloway, 1976: 92 (type information, generic transfer); Mineo, 1990b: 55 (synonymy); Johnson, 1992: 395 (cataloged, type information).
Gryon magneticus Galloway: Galloway & Austin, 1984: 79 (replacement name).
Gryon magneticum Galloway: Johnson, 1992: 387 (cataloged, type information).

***Hadronotus rufiventris* (Kononova), comb. nov.**
Paratype images: https://zenodo.org/record/5600439#.YXgbyPnMJaQ

Gryon rufiventris Kononova, 2001: 1469 (original description); Kononova & Petrov, 2002: 53 (keyed); Fabritius & Popovici, 2007: 14, 16 (description, keyed).
Gryon rufiventre Kononova: Kononova & Kozlov, 2008: 323, 343 (description, keyed).

***Hadronotus rugiceps* Ashmead, comb. rev.**
Holotype images in MBD: USNMENT00989865

Hadronotus rugiceps Ashmead, 1893: 231, 233 (original description, keyed); Brues, 1910: 47 (keyed); Kieffer, 1926: 454, 463 (description, keyed).
Gryon rugiceps (Ashmead): Muesebeck & Masner, 1967: 299 (generic transfer); Masner & Muesebeck, 1968: 36 (type information); Masner, 1983: 134, 155 (description, keyed); Johnson, 1992: 395 (cataloged, type information).

***Hadronotus rugosithorax* Ashmead, comb. rev.**

Hadronotus rugosithorax Ashmead, 1896: 799 (original description); Ashmead, 1900: 328 (distribution); Kieffer, 1926: 455, 467 (description, keyed).
Gryon rugosithorax (Ashmead): Masner, 1965: 78 (type information, generic transfer); Masner, 1976: 58 (description, systematic position); Johnson, 1992: 396 (cataloged, type information).

Comments. We transfer this species based on the original description which states "... the facial impression bounded by a raised margin, transversely striated."

***Hadronotus rugostriatus* (Dodd), comb. nov.**

Hadronotoides rugostriatus Dodd, 1920a: 352 (original description); Masner, 1965: 78 (type information); Johnson, 1992: 400 (cataloged, type information).

Comments. We transfer this species to *Hadronotus* based on characters from the original description, "Head transverse… coarsely densely rugose… scutum and scutellum very coarsely rugose."

***Hadronotus rugulosus* Fouts, comb. rev.**

Hadronotus rugulosus Fouts, 1934: 103 (original description).

Gryon rugulosus (Fouts): Bin, 1974: 463 (generic transfer, type information); Masner, 1976: 58 (description, systematic position).
Gryon rugulosum (Fouts): Mineo, 1983b: 286, 290 (description, emendation, keyed); Mineo, 1990a: 183 (variation); Johnson, 1992: 396 (cataloged, type information).

Comments. We transfer this species based on the original description, "...frons with a shallow antennal depression below, strongly transversely striate."

***Hadronotus samoensis* (Mineo), comb. nov.**

Gryon samoense Mineo, 1991: 8 (original description, assigned to *charon* species group).

Comments. This species is transferred to *Hadronotus* based on the original description and assignment to the *charon* group: "...the frontal depression are finely scabrous; this latter is transversely crossed by undulating wrinkles."

***Hadronotus sancti* (Mineo), comb. nov.**
Holotype images: https://zenodo.org/record/4521215#.YCGh2nlOlaQ

Gryon sancti Mineo, 1983c: 539, 546 (original description, keyed); Johnson, 1992: 396 (cataloged, type information).

***Hadronotus saxatilis* Kieffer, comb. rev.**
Holotype images: https://zenodo.org/record/4521231#.YCGjnnlOlaQ

Hadronotus saxatilis Kieffer, 1910: 293 (original description); Kieffer, 1912: 56 (redescribed as new, keyed); Kieffer, 1926: 454, 461 (description, keyed); Nixon, 1934b: 292, 293 (description, keyed); Risbec, 1950: 592 (keyed).
Gryon saxatilis (Kieffer): Masner, 1965: 78 (type information, generic transfer).
Gryon saxatile (Kieffer): Mineo, 1983b: 286, 291 (description, emendation, keyed); Mineo, 1990a: 184 (description); Johnson, 1992: 396 (cataloged, type information); Mineo & Caleca, 1994: 115 (distribution, biology).

***Hadronotus scapicompressus* (Mineo), comb. nov.**
Holotype images: https://zenodo.org/record/4521248#.YCGka3lOlaQ

Gryon scapicompressum Mineo, 1994: 123 (original description, assigned to *leptocorisae* group).

***Hadronotus scorsonis* (Mineo), comb. nov.**
Holotype images: https://zenodo.org/record/4521250#.YCGlUHlOlaQ

Gryon scorsonis Mineo, 1990a: 180, 181, 182 (original description, diagnosis); Johnson, 1992: 396 (cataloged, type information).

***Hadronotus scutellatus* (Masner), comb. nov.**

Gryon scutellatus Masner, 1979: 800, 792 (original description, keyed)

Comments. We transfer this species based on its placement in the *variicorne* group during its original description: "All 15 species described in this paper share the following characters in common… frontal depression very shallow… its sculpture consisting of a chain of transverse polygons above antennal insertion; clypeus small, receding, unarmed"

***Hadronotus scutidepressi* (Mineo), comb. nov.**
Holotype images: https://zenodo.org/record/4521254#.YCGl2XlOlaQ

Gryon scutidepressi Mineo, 1983b: 286, 292 (original description, keyed); Johnson, 1992: 396 (cataloged).

***Hadronotus semirufus* (Kononova), comb. nov.**

Gryon semirufum Kononova, 2005: 1356 (original description); Kononova, Pavlicek & Nevo, 2005: 814 (description); Kononova & Kozlov, 2008: 322, 341 (description, keyed).

Comments. We transfer this species to *Hadronotus* based on the original description, "The occiput is covered with arcuate wrinkles... The frontal depression is shallow, not bordered by an arcuate keel, shining, with lateral wrinkles..." Figures included in the publication clarify the description.

***Hadronotus sersis* (Mineo), comb. nov.**

Gryon serse Mineo, 1992: 24 (original description)

Comments. We transfer this species based on the original description, "Frontal depression moderately deep, large and topped, above the central keel crossed by coarse and moderately upcurved striae."

***Hadronotus sesbaniae* Risbec, comb. rev.**
Lectotype images: https://zenodo.org/record/4521276#.YFjH_K9KhaQ

Hadronotus sesbaniae Risbec, 1956: 247 (original description).
Gryon sesbaniae (Risbec): Mineo, 1980b: 214 (type information, generic transfer); Johnson, 1992: 396 (cataloged, type information).

***Hadronotus shisha* (Komeda & Mita), comb. nov.**

Gryon shisa Komeda & Mita, in Komeda, Mita, Hirose & Yamagishi, 2020: 124, 128 (original description, keyed).

Comments. Our generic transfer is based on images and characters in the original description.

***Hadronotus sibiricus* (Kononova), comb. nov.**

Gryon sibiricus Kononova, in Kononova & Petrov, 2001: 1472 (original description).
Gryon sibiricum Kononova: Kononova & Kozlov, 2008: 355, 322 (description, keyed); Timokhov, 2019b: 48 (catalog of species of Russia).

Comments. We transfer this species based on the original description, "The head is honeycomb... Frons with longitudinal carina, with distinct transverse wrinkles extending from this carina."

***Hadronotus sinop* (Masner), comb. nov.**

Gryon sinop Masner, 1979: 793, 802 (original description, keyed); Sarazin, 1986: 978 (type information); Johnson, 1992: 396 (cataloged, type information).

Comments. We transfer this species based on placement in *variicorne* group and original description: "frontal depression shallow but unusually well indicated by lateral and dorsal keels as well as sculpture consisting of several large transverse polygons above antennal insertion..."

***Hadronotus somaliensis* (Mineo), comb. nov.**
Holotype images: https://zenodo.org/record/4521278#.YCGp93lOlaQ

Gryon somaliense Mineo, 1983c: 540, 546 (original description, keyed); Johnson, 1992: 396 (cataloged).

***Hadronotus sponus* (Kozlov & Lê), comb. nov.**
Holotype images in MBD: IEBR 0138

Gryon sponum Kozlov & Lê, 1992: 235, 238 (original description, assigned to *muscaeforme* species group, keyed).
Gryon sponus Kozlov & Lê, 1996: 11 (description); Lê, 2000: 98, 133 (description, keyed, type information).

***Hadronotus stewarti* (Masner), comb. nov.**
Holotype images in MBD: CNC No. 17013

Gryon stewarti Masner, 1983: 134, 152 (original description, keyed); Sarazin, 1986: 979 (type information); Johnson, 1992: 396 (cataloged, type information).

***Hadronotus striatus* Dodd, comb. rev.**
Holotype images: https://zenodo.org/record/4521303#.YCGuonlOlaQ

Hadronotus striatus Dodd, 1913a: 155 (original description); Dodd, 1914d: 19 (keyed); Kieffer, 1926: 455, 470 (description, keyed); Galloway, 1976: 111 (type information, status uncertain); Johnson, 1992: 511 (cataloged, type information).

***Hadronotus strongist* (Kozlov & Lê), comb. nov.**
Holotype images in MBD: IEBR 0142

Gryon strongist Kozlov & Lê, 1992: 225, 227 (original description, assigned to *insulare* species group, keyed); 1996: 11 (description); Lê, 2000: 98, 134 (description, keyed, type information).

***Hadronotus sulawensis* (Mineo), comb. nov.**
Holotype images: https://zenodo.org/record/4521310#.YCGwo3lOlaQ

Gryon sulawense Mineo, 1990a: 181 (original description); Johnson, 1992: 397 (cataloged, type information).

***Hadronotus superbus* (Kononova), comb. nov.**
Holotype images: https://zenodo.org/record/5159846#.YQq2M0RKhaQ

Gryon superbus Kononova, 1984: 78 (original description); Kozlov & Kononova, 1989: 80 (keyed); Kozlov & Kononova, 1990: 268, 295 (description, keyed); Kononova & Petrov, 2002: 56 (keyed).
Gryon superbum Kononova: Johnson, 1992: 397 (cataloged, type information); Kononova & Kozlov, 2008: 328, 395 (description, keyed).

Comments. We transfer this species based on the original description, "The forehead is comparatively well pronounced, not limited to the keels, transversely striated," and images of the holotype female that illustrate the setose metapleuron, foveae along anterior T1, and an antenna with five clavomeres.

Hadronotus suvaensis Dodd

Hadronotus suvaensis Dodd, 1914d: 161 (original description); Dodd, 1915: 19 (keyed); Kieffer, 1926: 455, 470 (description, keyed).

Comments. We consider that this species belongs in *Hadronotus* based on the original description, "Face transversely rugulose."

Hadronotus testaceus (Subba Rao & Chacko), comb. nov.

Hadrophanurus testaceus Subba Rao & Chacko, 1962: 476, 480 (original description, keyed).
Gryon testaceum (Subba Rao & Chacko): Johnson, 1992: 397 (cataloged, type information).

Comments. We transfer this species based on the original description, "frons with a longitudinal shallow depression having transverse striations."

Hadronotus tetartus (Kononova), comb. nov.

Gryon tetartus Kononova, 2008: 325, 361 (original description, keyed).

Comments. We transfer this species based on characters from the original description, "Frontal impression superficial, with distinct longitudinal carina, transversely striated."

Hadronotus texanus (Kozlov & Kononova), comb. nov.

Holotype images: https://zenodo.org/record/4532088#.YCQyY3lOlaQ

Gryon texanum Kozlov & Kononova, 2004: 207 (original description); Kononova & Kozlov, 2008: 327, 382 (description, keyed); Timokhov, 2019a: 19 (distribution).

***Hadronotus titan* (Masner), comb. nov.**

Gryon titan Masner, 1979: 794, 801 (original description, keyed); Sarazin, 1986: 979 (type information); Johnson, 1992: 397 (cataloged, type information).

Comments. This species is transferred based on placement in *variicorne* group. From the original description, "All 15 species described in this paper share the following characters in common… frontal depression very shallow… its sculpture consisting of a chain of transverse polygons above antennal insertion; clypeus small, receding, unarmed."

***Hadronotus tonkinensis* (Kozlov & Lê), comb. nov.**
Holotype images in MBD: IEBR 0168

Gryon tonkinense Kozlov & Lê, 1992: 231, 237 (original description, assigned to *muscaeforme* species group, keyed).
Gryon tonkinensis Kozlov & Lê, 1996: 12 (description); Lê, 2000: 99, 135 (description, keyed, type information).

***Hadronotus triatomae* (Masner), comb. nov.**
Holotype images: https://zenodo.org/record/4521335#.YCG1anlOlaQ

Gryon triatomae Masner, 1975: 209, 211 (original description, keyed); Johnson, 1992: 397 (cataloged, type information).

***Hadronotus tricoloris* (Mineo), comb. nov.**
Holotype images: https://zenodo.org/record/4521343#.YCG2HnlOlaQ

Gryon tricolore Mineo, 1991: 16 (original description, assigned to *leptocorisae* species group).

***Hadronotus tridentatus* (Masner), comb. nov.**

Gryon tridentatus Masner, 1979: 793, 796 (original description, keyed); Sarazin, 1986: 979 (type information).
Gryon tridentatum Masner: Johnson, 1992: 397 (cataloged, type information).

Comments. This species is transferred based on placement in *variicorne* group. From the original description, "All 15 species described in this paper share the following characters in common… frontal depression very shallow… its sculpture consisting of a chain of transverse polygons above antennal insertion; clypeus small, receding, unarmed"

***Hadronotus tropicalis* Caleca, comb. nov.**
Holotype images: https://zenodo.org/deposit/4521357

Gryon tropicale Caleca, 1990a: 119, 132 (original description, keyed).

***Hadronotus unicolor* (Dodd), comb. nov.**
Holotype images: https://zenodo.org/record/4726101#.YInH1flKhaQ

Plastogryon unicolor Dodd, 1914a: 125 (original description); Dodd, 1915: 25 (keyed).
Plastogryon (*Heterogryon*) *unicolor* Dodd: Kieffer, 1926: 447, 450 (description, subgeneric assignment, keyed).
Gryon unicolor (Dodd): Galloway, 1976: 92 (type information, generic transfer); Johnson, 1992: 397 (cataloged, type information).

***Hadronotus urinius* (Kozlov & Lê), comb. nov.**
Holotype images in MBD: IEBR 0169

Gryon urinium Kozlov & Lê, 1992: 225, 227 (original description, assigned to *insulare* species group, keyed).
Gryon urinius Kozlov & Lê, 1996: 10 (description); Lê, 2000: 98, 136 (description, keyed, type information).

***Hadronotus urus* (Mineo), comb. nov.**
Holotype images: https://zenodo.org/record/4521361#.YCG3lHlOlaQ

Gryon urum Mineo, 1982b: 311 (original description); Mineo 1983a (keyed).

Comments. Transferred based on assignment to the *charon* species group. The holotype is lost.

***Hadronotus variicornis* Fouts, comb. rev.**
Holotype images in MBD: USNMENT00989867

Hadronotus variicornis Fouts, 1925: 149 (original description).

Gryon variicornis (Fouts): Masner & Muesebeck, 1968: 36 (type information, generic transfer); Masner, 1979: 793, 801 (description, keyed).
Gryon variicorne (Fouts): Johnson, 1992: 397 (cataloged, type information).

***Hadronotus varius* (Kozlov & Lê), comb. nov.**
Paratype images in MBD: USNMENT01197901

Gryon varium Kozlov & Lê, 1992: 229, 237 (original description, assigned to *muscaeforme* species group, keyed).
Gryon varius Kozlov & Lê, 1996: 11 (description); Lê, 2000: 99, 137 (description, keyed, type information).

***Hadronotus viggianii* (Mineo), comb. nov.**
Paratype images: https://zenodo.org/record/5037829#.YNoMzklKhaQ

Gryon viggianii Mineo, 1980b: 218 (original description, keyed); Johnson, 1992: 398 (cataloged, type information); Kononova & Petrov, 2002: 56 (keyed); Kononova & Kozlov, 2008: 331, 417 (description, keyed).

Comments. The original description is brief and inadequate for generic placement of this species. We transfer it to *Hadronotus* based on Figure II-3, which illustrates transverse striation on the frons, and our examination of a paratype specimen.

***Hadronotus vitripennis* (Masner), comb. nov.**
Holotype images in MBD: USNMENT01059242

Gryon vitripenne Masner, 1983: 135, 149 (original description, keyed); Johnson, 1992: 398 (cataloged, type information).

***Hadronotus watshami* (Mineo), comb. nov.**
Holotype images: https://zenodo.org/record/4521367#.YCG4uXlOlaQ

Gryon watshami Mineo, 1983c: 544, 546 (original description, keyed); Johnson, 1992: 398 (cataloged).

***Hadronotus watussus* (Mineo), comb. nov.**
Paratype images: https://zenodo.org/record/5037856#.YNoMiUlKhaQ

Gryon watussum Mineo, 1992: 20 (original description)

Comments. The description of this species is absurdly brief, but states, "the sculpture of the mesoscutum and scutellum that is all over strigose in *G. watussum* sp.n." and indicates that this species is morphologically similar to *G. hiberus* (=*H. hiberus*). This, in combination with examination of a paratype specimen, leads us to place it in *Hadronotus*.

***Hadronotus wintes* (Kozlov & Lê), comb. nov.**
Holotype images in MBD: IEBR 0171

Gryon wintes Kozlov & Lê, 1992: 224, 227 (original description, assigned to *insulare* species group, keyed); Kozlov & Lê, 1996: 10 (description); Lê, 2000: 97, 98, 139 (description, keyed, type information, synonymy).
Gryon thoum Kozlov & Lê, 1992: 224, 227 (original description, assigned to *insulare* species group, keyed).
Gryon thous Kozlov & Lê, 1996: 10 (description); Lê, 2000: 139 (junior synonym of *Gryon wintes* Kozlov & Lê).

***Hadronotus xanthosoma* (Masner), comb. nov.**
Holotype images in MBD: CNC No. 17017

Gryon xanthosoma Masner, 1983: 133, 164 (original description, keyed); Sarazin, 1986: 979 (type information); Johnson, 1992: 398 (cataloged, type information).

***Hadronotus yamagishii* (Mineo), comb. nov.**
Paratype images: https://zenodo.org/record/5037860#.YNoMZklKhaQ

Gryon yamagishii Mineo, 1981a: 143, 119 (original description, keyed)
Gryon maruzzae Mineo, 1981a: 134, 119 (original description, keyed); Komeda, Mita, Hirose & Yamagishi, 2020: 115 (junior synonym of *Gryon yamagishii* Mineo).
Gryon sugonjaevi Kozlov & Kononova, 1989: 78, 81 (original description, keyed); Kozlov & Kononova, 1990: 266, 274 (description, keyed); Johnson, 1992: 397 (cataloged, type information); Kononova, 1995: 81 (keyed); Kononova & Petrov, 2002: 54 (keyed); Kononova & Kozlov, 2008: 324, 354 (description, keyed); Komeda, Mita, Hirose & Yamagishi, 2020: 115 (junior synonym of *Gryon yamagishii* Mineo).

Comments. Images of the holotypes of *Gryon yamagishii* Mineo and *Gryon maruzzae* Mineo are available in Komeda et al. (2020).

***Hadronotus zimbabwensis* (Mineo), comb. nov.**
Holotype images: https://zenodo.org/record/4521373#.YCRZJHlOlaQ

Gryon zimbabwense Mineo, 1983c: 549, 551 (original description, keyed); Johnson, 1992: 398 (cataloged).

Phylogenetic placement of *Maruzza*

The concatenated alignment consisted of 493 taxa, 2,709 sites (base pairs plus gaps), and 31.9% missing data. *Maruzza japonica* was recovered in a moderately-supported clade composed of the *Psix*-group of genera (*Psix* Kozlov & Lê, *Paratelenomus* Dodd) and *Mantibaria* Kirby (58% UFBS) (Figure 95). This grouping was sister to *Hadronotus* (49% UFBS). In our initial phylogenetic analyses, the placement of *Mantibaria* was variable and we do not consider the genus to be a member of the *Psix*-group. This is the first phylogenetic analysis to include a species of *Maruzza*, and our results support its inclusion in the *Psix*-group of genera as proposed by Johnson (1985, 1988a).

Generic transfers to *Dyscritobaeus* Perkins

***Dyscritobaeus cates* (Kozlov & Lê), comb. nov.**
Holotype images in MBD: USNMENT01223667

Gryon cates Kozlov & Lê, 1992: 217, 221 (original description, assigned to *misellum* species group, keyed); Kozlov & Lê, 1996: 9 (original description); Lê, 2000: 96, 106 (description, keyed, type information).

***Dyscritobaeus cones* (Kozlov & Lê), comb. nov.**
Paratype images in MBD: USNMENT01197891

Gryon cones Kozlov & Lê, 1992: 217, 221 (original description, assigned to *misellum* species group, keyed).
Gryon comes Kozlov & Lê, 1996: 9 (description, misspelling); Lê, 2000: 96, 109 (description, keyed, type information).

***Dyscritobaeus ennius* Kononova & Fursov, comb. nov.**

Gryon ennius Kononova & Fursov, 2005a: 595 (original description); Kononova & Fursov, 2005b: 304 (description); Kononova & Kozlov, 2008: 329, 407 (description, keyed).

Comments. The arrangement of the ocelli in a relatively compact triangle and the shape of the metascutellum in Figure 4 of the original description provide the basis for transferring this species to *Dyscritobaeus*.

***Dyscritobaeus menerus* (Kozlov & Lê), comb. nov.**
Paratype images in MBD: USNMENT01223628

Gryon menerum Kozlov & Lê, 1992: 218, 221 (original description, assigned to *misellum* species group, keyed).
Gryon menerus Kozlov & Lê, 1996: 10 (description); Lê, 2000: 97, 122 (description, keyed, type information).

***Dyscritobaeus morinus* (Kozlov & Lê), comb. nov.**
Paratype images in MBD: USNMENT01223646

Gryon morinum Kozlov & Lê, 1992: 215, 220 (original description, assigned to *misellum* species group, keyed).
Gryon morinus Kozlov & Lê, 1996: 10 (description); Lê, 2000: 96, 125 (description, keyed, type information).

***Dyscritobaeus notoocellus* (Kozlov & Lê) comb. nov.**
Holotype images in MBD: IEBR 0172

Gryon notoocellum Kozlov & Lê, 1992: 215, 221 (original description, assigned to *misellum* species group, keyed).
Gryon notoocellus Kozlov & Lê, 1996: 9 (description); Lê, 2000: 96, 129 (description, keyed, type information).

Relationships in Gryonini

Tortorici et al. (2016) summarized various hypotheses of relationship between *Dyscritobaeus* and *Gryon*, some of which were not in agreement. Considering our findings, it is not surprising that competing ideas emerged about the phylogenetic proximity of these genera, given that results would vary widely if authors compared *Dyscritobaeus* to specimens of *Hadronotus* or *Gryon*. Our molecular analysis supports *Dyscritobaeus* as part of Gryonini, and it can easily be separated from *Gryon* by having five clavomeres, the absence of subgenual spines, a metapleuron with setation outside of the anterodorsal corner, and a non-striate axillula.

Both *Gryon* and *Dyscritobaeus* have a sublateral carina and lateral pit on T1. In their revision of Afrotropical *Dyscritobaeus*, Tortorici et al. (2016) did not mention the lateral pit on T1 per se, but essentially evaluated this character via the presence of the sublateral carina that is directly mesad (Figure 104). Interestingly, Tortorici et al. (2016) noted that these carinae are absent in four of the five brachypterous species that they treated. As part of this study, we examined a small number of *Encyrtoscelio* species and found a similar pattern. The sublateral carina and lateral pit are found in the macropterous *E. odorata* Kozlov & Lê (Figure 108) and are absent in a brachypterous species

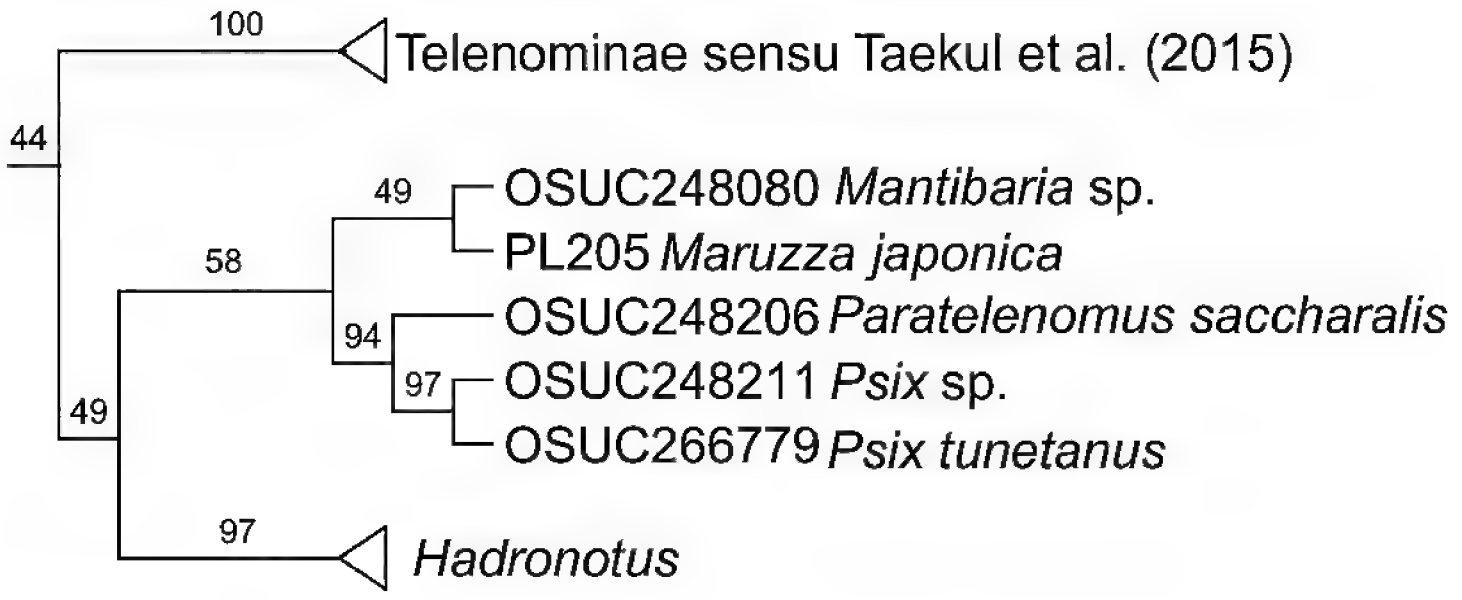


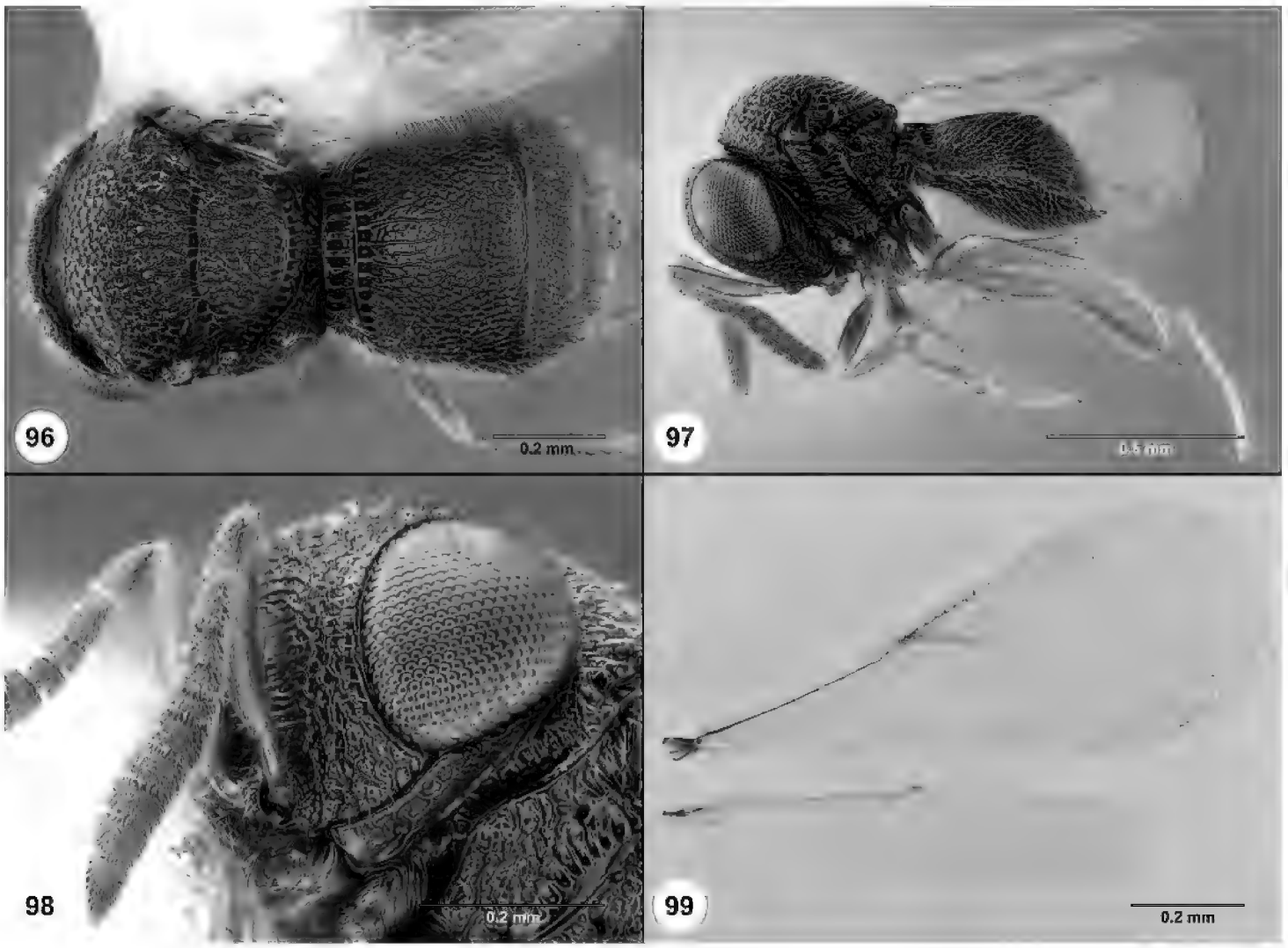
Figure 95. Phylogenetic placement of *Maruzza japonica* based on an expanded maximum likelihood phylogenetic analysis of the original multi-gene dataset (Figure 1) plus taxa for which only COI sequences were available. Values above branches indicate ultrafast bootstrap support values.

(Figure 109). To examine this pattern further, we imaged a specimen of the brachypterous *G. brevipenne* in a scanning electron microscope (Figures 113–116). This species has a striate axillula (Figure 113) and subgenual spines on the hind tibia (Figure 115), so we do not doubt its generic placement. The wings of *G. brevipenne* are reduced (Figure 113), but not as severely as the brachypterous *Encyrtoscelio* in Figures 109–110 or the brachypterous *Dyscritobaeus* in Tortorici et al. (2016), and it exhibits an intermediate level of reduction in other characters: the lateral pit on T1 is present, but the sublateral carina is absent (Figure 113); the claval formula is 1-2-2-1, whereas most *Gryon* have a 1-2-2-2 formula and the most reduced state is 1-2-2 (Figure 39). These findings suggest that the loss of structures on T1 is associated with living in leaf litter or a similar niche in which wings are not advantageous. The functional reasons are unknown, as the internal morphology associated with the structures on lateral T1 has not been examined. The brachypterous specimen of *Encyrtoscelio* that we examined has two subgenual spines on the hind tibia (Figure 111), indicating that this character is less susceptible to reduction. To our knowledge, all species of *Gryon* have either two or four subgenual spines, and their number may yield some phylogenetic signal. At present, we consider it unlikely that *Encyrtoscelio* is a lineage derived from within *Gryon*, as it can be separated by having five clavomeres (Figure 107), setation in the posterodorsal part of the metapleuron (Figure 109), and form of the axillula (Figures 108–109). However, this hypothesis remains to be formally tested.

Discussion

COI barcoding

Decentralized COI barcoding activities contribute to a global biodiversity research infrastructure that democratizes species identification to non-experts. This paradigm is



Figures 96–99. *Maruzza japonica* (FSCA 00094686, PL205 in Figure 95), female **96** habitus, dorsal view **97** habitus, lateral view **98** head and mesosoma, anterolateral view **99** wings, dorsal view.

especially valuable when researching understudied, hyperdiverse lineages of economic importance. Many surprising discoveries of regulatory and agro-economic consequence surely await to be found as these data accumulate and are analyzed at a global scale. The case of *G. aetherium* presented here illustrates, once again, the utility of COI barcodes for detecting and tracking the geographic spread of biological control agents under evaluation (Ganjisaffar et al. 2018; Stahl et al. 2019; Goltz et al. 2020). We suspect that there are many similar, yet undetected, cases to be found among already available barcode data. COI barcoding for platygastroids is rapidly expanding, with BOLD containing nearly 90,000 public barcode sequences for the superfamily. Almost 50,000 additional platygastroid barcodes are awaiting public release.

However, the utility of platygastroid COI barcodes is diminished by a lack of identified material. Only 357 species names have been applied to the approximately 90,000 public barcodes in BOLD. A huge portion of the available data are only identified to the family-level. Thus, we recommend that a primary research objective for the hymenopterist community should be to apply *at least* generic names to these public data whenever possible, either by examination of images associated with BOLD BINs or voucher specimens housed in collections.

A second concern is that the apparently widespread amino acid evolution in Scelionidae is, in part, causing COI barcodes in GenBank to be labeled as "unverified". This is due to the GenBank quality-control infrastructure being unable to confirm the

amino acid translations of submitted barcode sequences. This is consequential because unverified sequences in GenBank will not appear as hits in BLAST searches, potentially obfuscating the identification of uncommon genera or species. Further complicating matters, our small survey of scelionid COI barcode amino acids suggests that several protein phenotypes are present in the family. NCBI requires the following information to remove "unverified" labels in GenBank: 1) new sequences in fasta format, 2) sequencing technology and assembly program used, 3) properly formatted feature tables for the new annotations, and 4) an additional piece of supporting evidence such as: RID of BLAST analysis, multiple sequence alignments, peer-reviewed publications discussing the specific annotations, or evidence from wet-bench experiments. We recommend that the COI barcode annotations provided in this study be used to begin justifying the removal of the "unverified" comments in GenBank or prevent the label from being applied to newly gathered data.

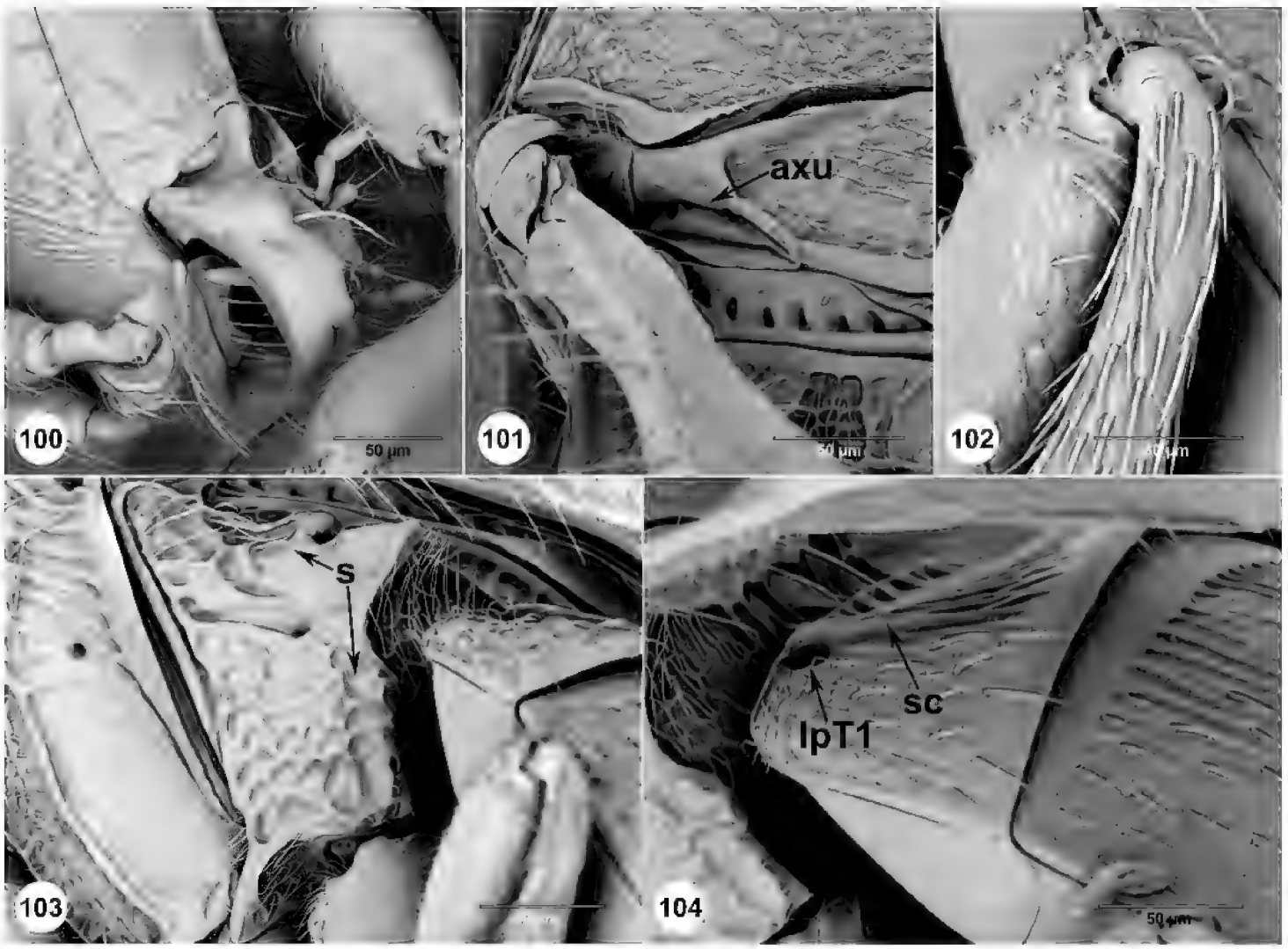
COI data analyzed in this study supported our identification of *Gryon aetherium* specimens. The success rate of COI identifications across *Gryon* and *Hadronotus* is not yet possible to determine, but preliminary results are promising. Terminal clusters appear to have divergences that could provide statistically supported identifications for many species and COI amino acid phenotypes supported our separation of *Gryon* and *Hadronotus*. Pentinsaari et al. (2016) suggested that the evolution of shortened COI sequences, and genomes more broadly, is associated with endoparasitic life histories. Whether the variable deletion of amino acids in COI loops in these genera is associated with differences in parasitoid biology would be a fascinating line of research.

Phylogenetics

Our ability to determine that *Gryon* and *Hadronotus* are separate lineages was facilitated by the dataset of Chen et al. (2021), which provided a framework for relationships throughout Scelionidae. In this regard, large-scale phylogenetic projects are invaluable for efficient completion of smaller analyses. Each of our molecular analyses retrieved Gryonini as sister to Telenominae sensu Taekul et al. (2014) and the *Psix* group was always retrieved outside of Gryonini+Telenominae, supporting the delimitation of Telenominae by Taekul et al. (2014). The analysis by Chen et al. (2021) retrieved *Gryon* as sister to *Dyscritobaeus*, but reexamination of the *Gryon* specimens in that study finds that they belong to *Hadronotus*. This is significantly different from our analyses, which did not recover *Dyscritobaeus* near *Hadronotus*. We suspect that this result was influenced by taxon sampling because the analysis of Chen et al. (2021) did not actually contain *Gryon* and our analyses focused intensely on *Gryon* and *Hadronotus*. Clearly, there remains much to be resolved regarding the systematics of these taxa.

Implications for biological control

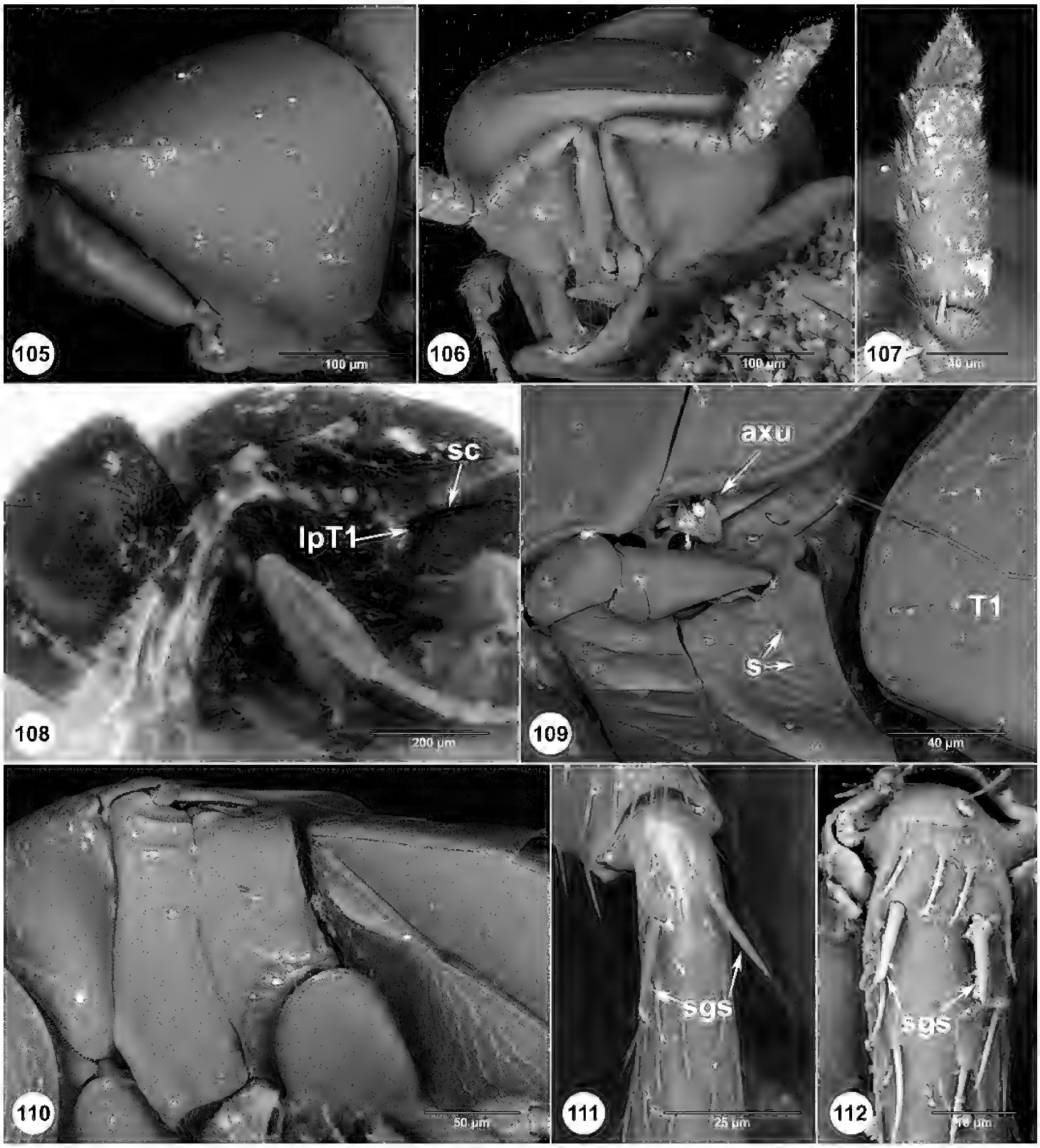
Detection of adventive *G. aetherium* in California and Mexico continues a trend of adventive scelionid biological control agents of stink bug eggs and emphasizes that



Figures 100–104. *Dyscritobaeus* sp. (USNMENT01335652) **100** mouthparts, ventrolateral view **101** scutellar-axillar complex, posterolateral view **102** hind femur and tibia, lateral view **103** mesosoma, lateral view **104** T1–T2, posterolateral view.

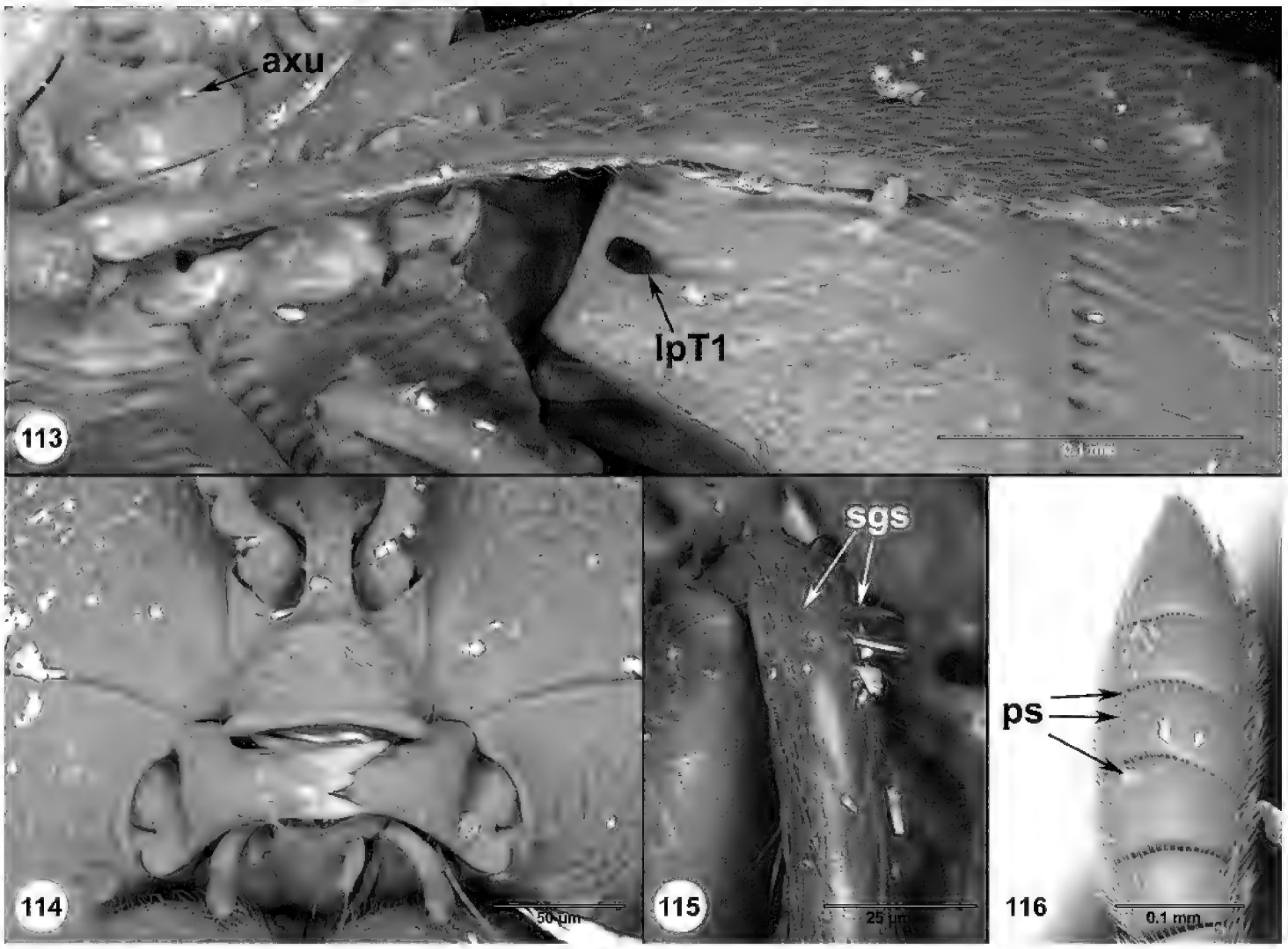
taxonomic preparedness is needed for rapid diagnoses. In the case of *G. aetherium*, similarities between species and unclear morphological limits contributed to a failure to recognize the adventive population in Mexico (Felipe-Victoriano et al. 2019), which would have accelerated measures to manage the pest. Instead, an incorrect name was applied to the species, as it was for quarantine populations (*G. gonikopalense*).

Despite the setbacks of these misidentifications, the taxonomy of *Gryon* and *Hadronotus* has advanced, and we here provide a sounder foundation for continued research. Our eventual identification of *G. aetherium* and determination of the quarantine and adventive populations of *G. aetherium* as conspecific are supported by multiple lines of evidence: molecular analysis, morphological comparison, and the interbreeding studies performed by Hogg et al. (2021). In the United States and Mexico, the arrival of *G. aetherium* provides new prospects for the management of bagrada bug and an opportunity to compare its biology under laboratory and field conditions. The detection of *G. aetherium* in Israel and South Africa via COI barcoding provided localities that are not yet known from collections. This, in turn, can inform the geographical breadth of specimens examined for alpha taxonomy and direct foreign exploration to regions that climatically match the invaded range and contain the biological control agent.



Figures 105–112. 105 *Encyrtoscelio* (FSCA 00094394), head, lateral view **106** *Encyrtoscelio* (FSCA 00094394), head, anterior view **107** *Encyrtoscelio* (FSCA 00094394), antenna, ventral view **108** *Encyrtoscelio odorata* (IEBR 0141), head and mesosoma, lateral view **109** *Encyrtoscelio* (FSCA 00094394), mesosoma and T1, dorsolateral view **110** *Encyrtoscelio* (FSCA 00094394), mesosoma and metasoma, lateral view **111** *Encyrtoscelio* (FSCA 00094394), hind tibia, posterior view **112** *Gryon* (CNC665446), hind tibia, posterior view.

As we have made progress, we have also exposed the magnitude of work that remains in *Gryon* and *Hadronotus*. Our molecular analyses of *Gryon* indicate that the current concept of *G. myrmecophilum* may represent a complex of cryptic species throughout the Nearctic region. Similarly, *Gryon* in Africa has many species that are challenging to separate by morphology alone. In *Hadronotus*, at least two species are known to be



Figures 113–116. *Gryon brevipenne* (OSUC 395663) **113** mesosoma and metasoma, dorsolateral view **114** mouthparts, anteroventral view **115** hind tibia, posterior view **116** antennal clava, ventrolateral view.

associated with bagrada bug, *H. karnalensis* from India (Chacko and Katiyar 1961) and an unidentified species from Kenya. We have yet to characterize the former and yet to attach a name to the latter. The images of primary types provided via this publication make it easier to identify species of *Gryon* and *Hadronotus* but are not a substitute for synthetic work that determines species limits and produces efficient identification tools. Our taxonomic efforts are ongoing and will undoubtedly inform a variety of biological control programs and ecological studies, including projects in the future and those that are underway.

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Supplementary material 1

GenBank accession number

Authors: Matthew R. Moore

Data type: Docx file.

Explanation note: Taxon sampling for multi-gene analysis and GenBank accession number.

Link: https://doi.org/10.3897/jhr.87.72842.suppl1

Supplementary material 2

Sequence data
Authors: Matthew R. Moore
Data type: Txt file.
Explanation note: Annotated COI amino acid sequences from exemplar scelionids.

Link: https://doi.org/10.3897/jhr.87.72842.suppl2

Supplementary material 3

Phylogenetic tree
Authors: Matthew R. Moore, Zachary Lahey, Elijah J. Talamas
Data type: Png file.
Explanation note: Maximum likelihood tree of scelionid COI data.

Link: https://doi.org/10.3897/jhr.87.72842.suppl3

Supplementary material 4

Table
Authors: Elijah J. Talamas
Data type: Xls file.
Explanation note: This table lists the morphological terms used in this publication and their associated concepts in the Hymenoptera Anatomy Ontology.

Link: https://doi.org/10.3897/jhr.87.72842.suppl4

Supplementary material 5

BOLD BINs

Authors: Elijah J. Talamas

Data type: Docx file.

Explanation note: BOLD BINs included in COI barcode analyses with their respective taxon identifications.

Link: https://doi.org/10.3897/jhr.87.72842.suppl5